MIGRATION DYNAMICS: TESTING ECOLOGICAL THEORY WITH TRACKING DATA FOR *AETHIA* AUKLETS IN THE NORTH PACIFIC

by

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Abstract:

Tracking technology has profoundly changed the study of spatial dynamics in marine vertebrates, enabling a large-scale focal-animal approach. This thesis shows that tracking data can be used, not only to characterize the annual migration cycle, but also to address ecological theory. I used geolocation tags (1g, 0.8-1.8% body mass) to investigate migration in a group of closely related seabirds. I found little evidence of negative effects of tags on Parakeet Auklets (*Aethia psittacula*), but tagged Whiskered Auklets (*A. pygmaea*) showed decreased chick growth, and reduced adult return rate. I combined tracking data with nest monitoring to test Ashmole's hypothesis that seabird populations are regulated by decreases in local food availability during the breeding season. If food was limiting, individuals should leave soon after breeding is completed. I found no evidence to support resource depletion in planktivorous auklets. Whiskered Auklets remained near the colony all year, and lag times for Parakeet and Crested (*A. cristatella*) auklets were up to 30 days. Interspecific differences were more consistent with differences in migration strategy than food availability. I also synthesized several aspects of migratory theory into a migratory continuum on which I placed my three species (using *a priori* knowledge about distribution, and behaviour) to develop and test predictions about migration distance, consistency, and winter habitat. Tracking data supported my classification of Whiskered (residents), Parakeet (intermediate migrants) and Crested auklets (long distance directed migrants). Crested Auklets had longer migration distances than Parakeet Auklets, and greater consistency in most measures of winter habitat use. Whiskered Auklet residence is likely enabled by their less seasonal

food supply, and night roosting to reduce metabolic costs. Crested Auklets' foraging style makes them more dependent on patchy aggregations of prey, which was reflected in their concentration in highly productive areas. Parakeet Auklets spent most of the year in the deep Aleutian Basin, where their flexible diet may allow them to subsist on gelatinous zooplankton and associated amphipods. Tracking data from comparative systems like this one have great potential for addressing ecological theory, while contributing to our understanding of different ways in which seabirds have adapted to the marine environment.

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List of Abbreviations and Symbols:

α – slope of linear regression line on a log-log plot of the initial phase of migration

ANCOVA – Analysis of co-variance

BRW – Biased random walk

CL – Confidence limits

CRAU – Crested Auklet

CRS – Carley R. Schacter

CV – Coefficient of variation

D – Deviance

dbar - Decibars

FMR – Field metabolic rate

GLM – General linear model

GME – Geospatial Modelling Environment software

IACC – Institutional Animal Care Committee

ILJ – Ian L. Jones

LDD – Long distance, directed (referring to migration)

N - Newtons

NPPSD – North Pacific Pelagic Seabird Database

NPRB – North Pacific Research Board

PAAU – Parakeet Auklet

pers. comm. – Personal communication

pers. obs. – Personal observation

rMSD – Root mean squared distance

SD – Standard deviation

UDOI – Utilization distribution overlap index

VC – Volume contour (often with subscript referring to a specific percent volume contour; *e.g.*,, VC_{50})

WHAU – Whiskered Auklet

χ^2 – Chi-squared

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CHAPTER 1: INTRODUCTION AND OVERVIEW

Migration has evolved in many taxa, usually as a strategy to survive in environments with a high degree of seasonality in resources (Boyle & Conway 2007, Dingle & Drake 2007, Shaw & Couzin 2013). It is an important component in the life history of these species, but has been difficult to study directly, relying on haphazard/opportunistic sightings, surveys at potential wintering grounds and stopover sites, and counts from first time captures at banding stations to determine the movement patterns of populations. This Eulerian approach (surveying the characteristics at a fixed point in space) results in 'snapshots' of high spatial and temporal resolution, but limited coverage, while providing limited or no information about migration dynamics of individual organisms. Over the last 30 years, the development of increasingly lightweight and inexpensive tracking technology has allowed unprecedented direct investigation of migration (Wakefield *et al.* 2009, McKinnon *et al.* 2013) in a Lagrangian frame of reference (following individuals or groups of individuals through a moving fluid; Schneider 1991). This individual-focused approach (Lande & Lewis 1989) allows us to describe the full annual cycle of migration in organisms of known age/sex/origin, although we sacrifice a certain amount of spatial accuracy due to limitations of the technology (Phillips *et al.* 2004, Wakefield *et al.* 2009). Despite the proliferation of tracking studies in recent years, most remain descriptive in nature (Bauer *et al.* 2009, McKinnon *et al.* 2013), seeking to map key wintering areas and stopover habitat. However, tracking data also have the potential to establish qualitative (Dingle & Drake 2007) and quantitative (Alerstam & Hedenstöm 1998) theories of migration on a firm empirical basis, a goal that has been limited by

availability of Eulerian data along the migration route (Bairlein 2003, Bauer *et al.* 2009, McKinnon *et al.* 2013).

Seasonal movements can take many forms, which may be usefully thought of as falling along a continuum of migratory behaviours (Dingle & Drake 2007, Cagnacci *et al.* 2011). At one end of the migratory continuum is the traditional view of migration, with all individuals travelling long distances from the breeding habitat to one or more distinct areas characterized by high winter productivity (*e.g.*,, Weng *et al.* 2008, Hedd *et al.* 2012, Lemke *et al.* 2013). At the other end is year-round residence in the breeding area (*e.g.*,, Ashmole 1962, Diamond 1975, McKnight *et al.* 2011). Dispersive migration is an intermediate strategy, with individuals spreading out from the breeding site in many directions, or simply moving to different habitat in the general vicinity of the breeding site (*e.g.*, Harris *et al.* 2010, Hatch *et al.* 2010, Hedd *et al.* 2011). Migrations can also be classified as obligate (individuals must migrate) or facultative (individuals 'choose' to migrate based on local conditions), although these are also more likely to be extremes on a continuum than a true dichotomy (Berthold 1975, Terrill 1990, Newton 2012). Obligate migrations (usually long-distance, directed migrations) are characterized by consistency in timing and destination among individuals (Newton 2012). Departure from the breeding ground is preemptive, occurring before local conditions deteriorate, while food is still plentiful enough to build sufficient fuel stores for the journey (Berthold 1975, Terrill 1990, Newton 2012). Obligate migrations typically have a strong genetic component, with timing determined by an endogenous circannual rhythm, which can be adjusted based on external cues (such as photoperiod) that forecast future declines in local

resources (Berthold 1975, Alerstam 1978, Terrill 1990). Facultative migrations (usually short-distance and/or dispersive) are more variable, and are under less rigid genetic control (Newton 2012). Departure is triggered directly by changes in local conditions (*e.g.*,, food availability, temperature, weather, *etc*.; Terrill 1990, Newton 2012), with each bird responding according to an internal threshold based on their individual condition, energetic requirements, *etc*. (Chapman *et al.* 2011, Newton 2012).

Attempts at a quantitative framework for the study of migration have largely focused on birds, combining optimization analysis (Maynard Smith 1978, Stephens & Krebs 1986), with predictions based on flight mechanics (Pennycuick 1975, 1978). Optimal migration theory (Alerstam & Hedenström 1998, Hedenström 2008, Alerstam 2011) assumes that selection is operating on the individual to minimize time spent travelling, net energy expenditure, or mortality risk (Alerstam 2006, Gudmundsson *et al.* 1991, Schmaljohann *et al.* 2009). These models have been used to evaluate many different aspects of migratory behaviour, including migration routes, timing of departure and arrival, and phenotypic flexibility (Alerstam 2001, 2011, Newton 2006, Shaw & Couzin 2013). Much work has focused on the energetics of food intake during the migration journey and how this affects stopover use (*e.g.*,, Lindström 1991, Gudmundsson *et al.* 1991). Energy-selected migrants are expected to make frequent stops, carrying a lower fuel load to minimize the energy-cost of carrying extra weight (Alerstam & Lindström 1990). Time-selected migrants, on the other hand, should make longer trips and fewer stopovers, paying a higher energy cost to minimize the overall duration of the migration (Alerstam & Lindström 1990). Optimal migration theory can be

useful to evaluate the relative importance of different selective forces, as a means to generate testable hypotheses for empirical studies of migration, and to forecast the effects on migration of climate change and habitat loss (Weber et al 1999, Bauer *et al.* 2009). However, many factors can lead to actual or apparent sub-optimality in migration behaviour, including compromise between different optimization factors to maximize overall fitness (Southwood 1977, Dingle 2006, Newton 2007), and phylogenetic constraints on anatomy and behaviour. To date, the application of tracking data to test predictions of optimal migration theory has been mostly focused on investigation of the role of wind in the determination of migration routes (*e.g.*,, Åkesson & Hedenström 2000, Thorup *et al.* 2003, González-Solis *et al.* 2009), although some recent studies have taken a broader approach, looking at migration routes, timing, and stopover use (*e.g.*,, Schmaljohann *et al.* 2012).

Kölzsch & Blasius (2008) proposed a framework, based on statistical mechanics (advection-diffusion models; Okubo 1980), to describe avian migration dynamics. This Lagrangian approach, under the name of individual-based modeling, has a history of application in biological oceanography, most notably with passively drifting organisms (Lande & Lewis 1989). Kölzsch & Blasius (2008) found that migrating storks use rapid, directed, ballistic motion at short time scales, and slower, more diffusive motion at seasonal time scales. With this approach, the regression of root mean squared displacement (km) on time (days) is used to quantify the degree of diffusive motion (km/day). We can extend this idea, and use it to help categorize migrations based on the type and extent of movements in annual migration tracks. Periodic ballistic or

directionally biased super-diffusive movement, interspersed with relatively stationary interludes at wintering areas or stopover sites (Kölszch & Blasius 2008), corresponds to the classical view of long-distance, directed migration, while diffusive/sub-diffusive movement away from the breeding site corresponds to a more dispersive type of migration. Residents would be expected to show minor diffusion away from the breeding site (foraging movements), with a daily reset to the point of origin (if returning to a fixed winter territory or roosting site).

In addition to the direct study of migration, tracking data also have the potential to address related ecological questions, such as population regulation. The study of population regulation began with theoretical/speculative work by David Lack (1954, 1966, 1968), focusing on evidence available at the time from studies of migrating birds. He concluded that most populations are stable, tending to fluctuate within very restricted limits, and that this stability could only be produced by density-dependent factors (Lack 1954). When, in the annual cycle, this regulation occurs is less clear. Lack hypothesized that bird populations were most likely limited by food availability in winter, although this was based mainly on data from songbirds wintering at high densities in a limited area (intense competition), or on indirect evidence from the partitioning of winter habitat and/or diet in closely related species (Lack 1954, 1968). Ashmole (1963, 1971) elaborated on Lack's work, focusing on the case of seabirds. He argued that seabird demography is driven by their colonial breeding strategy. During the breeding season they are constrained to forage within a certain distance of the colony by the need to return to incubate and/or provision their offspring. Once released from these constraints, they

are free to seek better foraging elsewhere, or to remain near their feedings grounds full-time (Ashmole 1963, Mackley *et al.* 2010). Therefore, Ashmole (1971) postulated that any density-dependent effects regulating seabird populations must be operating at the colony, mediated by density-dependent changes in food availability, especially in tropical habitats that do not experience the seasonal increases in productivity seen at higher latitudes. Specifically, Ashmole (1963) proposed that the concentration of individuals with high nutritional needs (increased due to need to produce eggs, provision offspring, *etc*.) in a limited area will lead to a decrease in the local availability of food ("Ashmole's Halo", Birt *et al.* 1987), either due to depletion of resources in the vicinity of the colonies, or interference competition from large numbers of foraging birds resulting in decreased accessibility of prey (Ashmole 1963, Furness & Birkhead 1984, Birt *et al.* 1987). However, to my knowledge, only one study has directly demonstrated food depletion (of sedentary benthic fish) around a seabird colony (Birt *et al.* 1987). A number of studies have compared large and small colonies, and found results consistent with density-dependent population regulation at the colony (*e.g.*,, Furness & Birkhead 1984, Hunt *et al.* 1986, Lewis *et al.* 2001), but it is not clear whether such effects are due to resource depletion, interference competition, or some other factor. Modelling studies have shown that the food demands of piscivorous seabirds can amount to a substantial fraction of the standing stock of prey around a colony (*e.g.*,, Wiens & Scott 1975, Furness & Cooper 1982). However, these publications do not take into account advective resupply of prey into the region, which has been shown to be at least as large as rates of removal due to energetic demands by a colony (Bourne 1983, Schneider *et al.* 1992).

Advective resupply is likely an important factor in most systems, especially for planktivorous species (Springer *et al.* 1989, Springer *et al.* 1996, Piatt & Springer 2003). Tracking data can add to our understanding of population regulation, by allowing for more direct measurement of individual foraging effort during the breeding season (*e.g.*,, Elliott *et al.* 2009, Gaston *et al.* 2013, Oppel *et al.* 2015) and post-breeding behaviour once birds are released from the constraint of foraging near the colony.

Migration in seabirds has evolved to maximize the year-round survival of individuals in a seasonal marine environment, where resources are spatially and temporally heterogeneous, but predictably distributed (Southwood 1977, Weimerskirch 2007). Seasonality of resource needs is magnified by the fact that typical feeding habitat at sea is unsuitable for reproduction, producing a seasonal need to aggregate at breeding colonies, usually in coastal areas or on remote oceanic islands with few predators (Ashmole 1971). Once breeding is completed, seabirds (like other marine predators) converge on oceanic 'hotspots', where a combination of winds, water currents, and changes in bottom topography serve to concentrate nutrients and enhance both primary productivity and aggregations of prey near the surface (reviewed in Schneider 1991). Seasonal effects are pronounced in the Bering Sea, where ice cover is unpredictable in winter, except for southern regions such as the Aleutian Islands. Winter seabird abundances are especially high in Aleutian passes, and along the shelf break, where strong currents and localized upwelling provide reliable concentrations of accessible zooplankton (Schneider et al 1987, Springer *et al.* 1996, Hunt 1997, Ladd *et al.* 2005, Suryan *et al.* 2006). Diving seabirds are more likely to be dependent on these productive

hotspots (Wahl *et al.* 1989) than surface feeders, because they expend more energy in transit between foraging locations, and during foraging itself (Ainley *et al.* 1984). This is likely due to morphological adaptations for diving (especially in wing-propelled divers), which result in less efficient flight (Pennycuick 1987, Thaxter *et al.* 2010, Elliott et al. 2013) and therefore higher energy requirements. Soaring surface feeders spend less energy on flight and can afford to roam widely, feeding on less spatially predictable prey (Schneider *et al.* 1986, Sato *et al.* 2007).

Historically, the study of seabirds at sea has been largely limited to the use of ship-based surveys (Eulerian approach). These surveys collect valuable data about winter distributions at the species level, but provide no information about the colony-of-origin of sighted birds, or the migration dynamics of individual birds. Ship-based surveys also tend to have large gaps in spatio-temporal coverage due to the expense of ship time and a reduction of survey effort in winter. Over the last 30 years, the use of tracking devices (tags) has grown rapidly, allowing the tracking of known individuals over time (Lagrangian approach) and study of their habitat use and migratory behavior (Vandenabeele *et al.* 2011). In particular, the ongoing development of light-weight and inexpensive archival geolocation tags (DeLong *et al.* 1992, Wakefield *et al.* 2009, Wilson and Vandenabeele 2012) is allowing deployment on smaller species and at higher sample sizes for more robust analyses. However, extra weight and/or drag of tracking tags may make it more difficult for birds to forage and make it more energetically expensive to travel (Barron *et al.* 2010, Vandenabeele *et al.* 2012). Therefore, it is important to

evaluate potential effects of tags in any tracking study to allow us to weigh the value of the resulting data, and assist with their interpretation.

Aethia auklets breeding in the Aleutian Islands of Alaska provide an excellent system for a comparative study of migration. They are small, pursuit-diving seabirds with high metabolic demands (Johnson & West 1975), creating strong selection pressure to locate and exploit the most abundant and reliable sources of prey. They breed at shared colonies in some parts of their range (including our study sites on Buldir and Gareloi islands), and while their breeding-season biology has been well-studied (*e.g.*,, Knudtson & Byrd 1982, Hipfner & Byrd 1993, Hunter *et al.* 2002), very little is known about their migration dynamics, or other aspects of their ecology for the majority of the year. The three congeners studied here differ markedly in aspects of their behaviour and morphology, which suggest several productive avenues of comparative analysis. Whiskered Auklets are nocturnal (in the Aleutian and Commander islands), and feed in tide rips within 16 km of shore (Byrd & Gibson 1980). They breed at many small colonies throughout the Aleutians (Byrd *et al.* 2005), and remain near the islands year-round (Byrd & Williams 1993, NPPSD 2015). Crested Auklets breed at much higher densities and forage in large flocks offshore (Bédard 1969, Gaston & Jones 1998, Byrd *et al.* 2005), where they feed on a specialized diet dominated by euphausiids and calanoid copepods (Hunt *et al.* 1998, Guy *et al.* 2009, Bond *et al.* 2011b). Parakeet Auklets breed at lower densities (Byrd *et al.* 2005), and are less gregarious, flying out from colonies to forage singly or in small groups (Gaston & Jones 1998). They also have a more generalist

diet, including mollusks, gelatinous zooplankton, euphausiids, copepods, and larval fish (Day & Byrd 1989, Harrison 1990, Hunt *et al.* 1998).

The aim of this thesis is to take advantage of recent developments in lightweight tracking technology (geolocation tags; DeLong *et al.* 1992, Wakefield *et al.* 2009, Wilson & Vandenabeele 2012) to investigate the full annual cycle of migration, using a group of closely related seabirds (*Aethia* auklets) as a model system. I experimentally evaluate potential negative effects of the tracking tags on my study species (Chapter 2; Schacter & Jones 2017) in order to validate the interpretation of the resulting tracking data. I then use tracking data to provide the first complete picture of the annual distribution of Whiskered (Chapter 4) and Parakeet auklets (Chapter 5), and compare these data with that collected for Crested Auklets by K. F. Robbins (unpublished data) to test predictions derived from theories of population regulation in migrant species (Chapter 2), and migration dynamics when no longer constrained to breeding sites (Chapter 5).

In Chapter 2 I highlight what I believe to be a general weakness in the field of tracking research. When designing studies to answer biological/ecological questions, scientists must keep in mind that their actions can change the characteristics or behaviors being measured (*i.e.*, observer effects; Sykes 1978, Wilson and Vandenabeele 2012). There are also ethical considerations, and any negative effect (*e.g.*, pain, stress, or mortality) on study subjects should be considered relative to the value of the data obtained (Vandenabeele *et al.* 2011, Animal Behaviour 2012). Many tracking studies include only a cursory investigation of tag effects, if any (reviewed by Vandenabeele *et al.* 2011), making it difficult to evaluate the biological relevance of their results. A

general guideline, developed for albatrosses and petrels, proposes that tags should be ≤ 3% body mass to avoid negative effects (Phillips *et al.* 2003). This guideline has since been broadly applied to many other taxa. However, auklets (and alcids in general) may be less tolerant of extra weight and/or drag than other species because their wings are adapted for underwater pursuit-diving and so flight is energetically expensive (Pennycuick 1987, Obrecht *et al.* 1988, Vandenabeele *et al.* 2012). Studies of small alcids have shown negative effects of tags ≤ 3% body mass (Ackerman *et al.* 2004, Whidden *et al.* 2007, Elliott *et al.* 2010), and previous work on Crested Auklets (one of the most highly migratory members of the genus) showed strong effects of a tag weighing 1% body mass on several aspects of reproduction and behavior (Robinson & Jones 2014). Because tracking data form the basis of all subsequent chapters, it is important to first assess the potential negative effects of tagging in these species, and then factor in that information when interpreting all results. I conducted a controlled experiment to investigate the effect of tags on adult return rate, reproductive success, and chick growth in Whiskered and Parakeet auklets compared to untagged control birds (Crested Auklet data are presented in detail elsewhere: Robinson & Jones 2014, KF Robbins unpublished data). I also reviewed the literature to evaluate whether the commonly accepted guideline (that tags should not exceed 3% body mass) should continue to be broadly applied across seabird taxa.

In Chapter 3 I use tracking data in a novel way to test predictions relating to food depletion around seabird colonies ('Ashmole's Halo'; Birt *et al.* 1987), and discuss the possibility of food depletion as a driver of migration in planktivorous species. Ashmole

(1963) postulated that any density-dependent effects regulating seabird populations operate at the colony, and most likely involve the availability of food (Ashmole 1971). Specifically, Ashmole (1963) proposed that the concentration of breeding individuals with high nutritional needs in a limited area will lead to a near-colony reduction in the availability of food. If so, the resulting increase in foraging effort required could serve as a proximate cue triggering post-breeding migration in some species. To my knowledge, only one study has shown direct evidence of reduced prey densities (of sedentary benthic fish) near seabird colonies (Birt *et al.* 1987). Others have attempted to address the question in piscivorous seabirds, using indirect methods such as measurements of chick growth or foraging effort, or calculations of energy demands (*e.g.*, Wiens & Scott 1975, Hunt *et al.* 1986, Elliot *et al.* 2009). However, calculations of energy demand do not take into account the influence of advective resupply or migratory passage of prey. Advective resupply has been shown to be comparable to rates of consumption based on food demand by a colony (Bourne 1983, Schneider *et al.* 1992), and is likely to be an important factor, especially for planktonic prey. The lateral distribution of zooplankton, unlike most fish species, is determined mainly by passive transport, and concentration by features of the local oceanography (currents, fronts, upwelling, *etc*.; Mackas *et al.* 1985, Schneider 1991). Bering Sea currents provide a constant input of new prey to replace those consumed (Springer *et al.* 1996, Piatt & Springer 2003), making significant food depletion unlikely (Bourne 1983, Schneider *et al.* 1992). If food is an important limiting factor at the colony (whether due to food depletion, or interference competition), individuals of all species should leave as soon as possible once released from the need to

return to the colony to incubate/provision their offspring. To investigate how three species of *Aethia* auklets differ in their response to being released from this constraint, I combined monitoring of individual reproductive timing with tracking data obtained from geolocation tags deployed on those same individuals (to determine the date of departure from the colony). I used these data to determine the amount of synchrony in migration within species, and the amount of lag between breeding cessation and onset of migration. Species with the highest metabolic demands (*i.e.,* Whiskered Auklets) should be under the most pressure to seek out better food sources away from the colony, and species with a greater potential to impact their food supply (*i.e.,* Crested Auklets breeding at higher densities with a more restricted diet) should benefit more by leaving than generalist feeders breeding at lower densities (*i.e.,* Parakeet Auklets). I also predict that, given their more directed, long-distance migration (Robinson 2015, K.F. Robbins unpublished data), Crested Auklet departure patterns will show a greater degree of synchrony and consistency in timing (consistent with obligate migration) than will the more dispersive Parakeet Auklets.

In Chapter 4 I use data from geolocation tags to confirm the degree to which Whiskered Auklets remain resident at the colony year-round. This species has been named a species of conservation concern, and is considered especially vulnerable to oil spills, invasive mammalian predators, and other threats due to its restricted distribution and its year-round presence in Aleutian passes (Troy & Bradstreet 1991, Troy 1991, Williams *et al.* 2003, NPRB 2005). There have been anecdotal reports for many years of adults and juveniles returning to the islands periodically in winter (*e.g.,* Stejneger 1885,

Murie 1936, Byrd & Gibson 1980, Zubakin & Konyukhov 2001), and ship-based surveys show that Whiskered Auklet winter distribution at sea is largely restricted to areas within a few kilometres of the Aleutian Islands (Byrd & Williams 1993, NPPSD 2015). However, winter survey coverage is limited (NPPSD 2015), and provides no information as to the colony-of-origin of sighted birds. Tracking technology has only recently progressed to the point where devices can be deployed on a bird of this size, allowing measurement of the non-breeding movements and behaviours of known individuals (Wilson & Vandenabeele 2012). I investigated the wintering strategy of Whiskered Auklets breeding at Buldir Island, using a combination of tracking data (to map winter distribution), behavioural data (sea water immersion sensors on tags to detect potential roosting on land), and audio recordings at the colony (to confirm year-round presence near breeding sites).

In Chapter 5 I synthesize migratory theory into a continuum concept, and use the placement of three congeneric species on that continuum to develop and test predictions concerning migratory distance and velocity, and consistency of destination, distance travelled, and habitat use. I also provide the first description of migration and winter distribution of Parakeet Auklets. I build on results from previous chapters to propose the placement of three *Aethia* auklet species on a continuum of migratory behaviour (Fig. 5-1) from long-distance, directed (LDD) migration (Crested Auklets) to intermediate migration (Parakeet Auklets) to residence (Whiskered Auklets), based on *a priori* knowledge about their ecology, behaviour and morphology. Seasonal movement patterns of animals range in extent from long-distance migration between distinct regions, to year-

round residence, with more short-distance, dispersive migrations in between. There is also a continuum of migration type, from obligate migration (individuals must migrate), to facultative migration (extent of migration depends on local conditions) to obligate residence. Obligate migrations have a strong genetic component, and are typically LDD migrations, characterized by consistency in timing and destination. Facultative migrations are generally short-distance and/or dispersive, more variable in timing and destination, and are under less rigid genetic control. On a quantitative level, migrations can also be classified on a continuum based on distance travelled over time, from ballistic (highly directional, covering long distances across a barrier) to super-diffusive (directionally biased movement), to sub-diffusive (more random dispersal). I synthesized these aspects of migratory theory into an integrated migratory continuum from LDD migration, to intermediate migration, to residence. Based on the above placement, I predict Crested Auklets (LDD migrants) will travel greater distances, with greater consistency in destination, distance travelled, and habitat used than Parakeet Auklets (Terrill 1990, Newton 2012). Interspecific differences are also predicted based on the diffusive/ballistic continuum (Fig. 5-C). I expect Whiskered Auklets (residents) to show only limited diffusive movement away from the colony (due to daily foraging movements and/or tag error), Parakeet Auklets to make mostly diffusive/sub-diffusive movements (slow travel while foraging), and Crested Auklets to show super-diffusive movement, as a consequence of periodically strong directional movements toward seasonally predictable foraging hotspots. Due to their more specific diet and larger flock sizes, I also predict that Crested Auklets will be more dependent on hotspots with high prey availability (*e.g.*,

shelf/shelf-break region, northern regions where long days lead to high primary productivity during the ice-free season) and show characteristics of time-selected migration (rapid travel between a small number of suitable stopover locations) to maximize use of this habitat before it is covered by ice. This strategy should be apparent in behavioural data as longer bouts of flight with fewer stopovers during the autumn migration (Alerstam & Lindström 1990, Alerstam & Hedenström 1998), represented by greater weekly flight velocities and longer bouts of dry readings on tag sensors. Parakeet Auklets, which feed on a wider range of prey with more stable annual abundances, should be less reliant on foraging hotspots (Bédard 1969, Hunt *et al.* 1993), and less likely to be time-selected.

Co-authorship Statement:

I took the lead on all practical aspects of data collection (tagging protocols and deployment, monitoring procedures, *etc*.), conducted all fieldwork (with the help of several field assistants, including Ian L. Jones) and data analysis, and was the primary author for all chapters of the thesis.

Chapter 2 was co-authored with Ian L. Jones (see above), who proposed the larger tracking project of which my thesis is a part (North Pacific Research Board Project 1212), and who provided assistance in the field, and edits to the manuscript. Chapter 2 has been accepted for publication: Schacter, C.R. and I.L. Jones (2017). Effects of geolocation tracking devices on behavior, reproductive success and return rate of *Aethia* auklets: an evaluation of tag mass guidelines. The Wilson Journal of Ornithology 129:459-468.

Chapter 3 was developed collaboratively by myself and David C. Schneider. I collected, processed, and analyzed all data for Parakeet and Whiskered auklets, with Crested Auklet data for comparison provided by Katherine F. Robbins, who also participated in extensive brainstorming during data processing and analysis. David C. Schneider proposed the topic for this chapter, and assisted with data analysis and editorial advice during manuscript preparation.

Chapter 4 was based on work originally proposed by Ian L. Jones as part of NPRB Project 1212 (see Chapter 2 above).

Chapter 5 was developed by myself, in collaboration with David C. Schneider, who made substantial suggestions for the theoretical approach to the interspecific comparison, assisted with data analysis, and provided editorial advice. Crested Auklet data were provided by Katherine F. Robbins, who also participated in extensive brainstorming during data processing and analysis. The description of Parakeet Auklet migration was originally proposed by Ian L. Jones (NPRB Project 1212).

CHAPTER 2: EFFECTS OF GEOLOCATION TRACKING DEVICES ON BEHAVIOUR, REPRODUCTIVE SUCCESS AND RETURN RATE OF *AETHIA* AUKLETS: AN EVALUATION OF TAG MASS GUIDELINES

Abstract

The use of tracking devices (tags) to investigate seabird movements and habitat use has grown rapidly over the last 30 years. However, often tracking data are often reported without assessment of the effects of tags. Attachment of extra mass and bulk risks altering behavior, and effects likely vary depending on the size, anatomy, and foraging strategy of different species. A guideline that tags should not exceed 3% body mass is widely accepted by seabird researchers, but this guideline was developed for albatrosses and petrels. A review of tracking studies showed that alcids are more likely to be affected by tags than other groups. We found some evidence of a negative effect of tags on Parakeet Auklets' (*Aethia psittacula*; mean mass 266g, tag 0.8-1.1% of body mass) reproductive success, but not return rate or chick growth. Tagged Whiskered Auklets (*A. pygmaea;* mean mass 112g, tag 1.8% of body mass) showed minor decreases in chick growth, and a 74% lower adult return rate during 2014-2015, despite no significant difference from control returns in 2013-2014. Our study demonstrated negative effects in alcids of tags well below the 3% guideline, confirming that limits for one group should not be uncritically applied to all seabirds. Mass of tags deployed should be kept to a minimum, but other factors (*e.g.*,, wing-loading, flight energetics, foraging strategy) may be equally important. To ensure the biological relevance of collected data, we strongly recommend that inclusion of tag effect experiments be considered essential in the design and approval of tracking studies.

Introduction

When designing studies to answer biological/ecological questions, scientists must keep in mind that their actions can change the characteristics or behaviors being measured (*i.e.*, observer effects; Sykes 1978, Wilson and Vandenabeele 2012). There are also ethical considerations, and any negative effect (*e.g.*, pain, stress, or mortality) on study subjects should be considered relative to the value of the data obtained (Vandenabeele *et al.* 2011, Animal Behaviour 2012). This issue has become increasingly relevant in seabird research as the use of tracking tags for studies of habitat use and migratory behavior has grown rapidly in the last 30 years (Vandenabeele *et al.* 2011). In particular, the development of light-weight and inexpensive archival geolocation tags (DeLong *et al.* 1992, Wakefield *et al.* 2009, Wilson and Vandenabeele 2012) is allowing deployment on smaller species and at higher sample sizes for more robust analyses. However, extra weight and/or drag of tracking devices (hereafter referred to as 'tags') may make it more difficult for birds to forage and energetically expensive to travel (Barron *et al.* 2010, Vandenabeele *et al.* 2012).

Many tracking studies include only a cursory investigation of tag effects, if any (review by Vandenabeele *et al.* 2011), making it difficult to evaluate the biological relevance of their results. Based on a review of effects on various species of albatrosses and petrels across 20 studies, Phillips *et al.* (2003) proposed a maximum guideline of ~3% body mass for tags, but it is unclear how well their recommendations apply to other groups of seabirds that rely more on diving for prey (*e.g.*,, Auks/Alcidae and Diving Petrels/Pelecanoididae). For diving seabirds (foot-propelled, or wing-propelled with feet

extended for use as a rudder), any effect may be magnified by increased drag in the much denser sea water (relative to air) in which the birds forage. Streamlined wings adapted for propulsion underwater also lead to greater wing-loading and more energetically expensive flight (Pennycuick 1975, 1987), which could make those species more susceptible to effects from added mass (Elliott *et al.* 2014). Nevertheless, Phillips *et al.*'s (2003) review is commonly cited as a justification for tagging a wide range of species, often without any attempt to validate this guideline for the species in question (*e.g.*, McKnight *et al.* 2013, Hennicke *et al.* 2015, Weimerskirch *et al.* 2015). Alternatively, many studies cite a lack of detrimental effects in previous research on their focal species or closely related taxa, but do not take into account temporal or geographic differences in local conditions that can have significant impact on the effects of tags, through changes in individual condition or parental investment (Pugesek & Diem 1990, Heggøy *et al.* 2015). A recent meta-analysis of tag effects in shorebird geolocation studies showed negative effects of devices above 1.5% body mass, and high variation among breeding sites within species, suggesting that local factors may be important (Weiser *et al.* 2016).

Aethia auklets are a group of small (80-300g), planktivorous seabirds that breed in large numbers in the Bering Sea and Sea of Okhotsk. Their high breeding site fidelity (Zubakin and Zubakina 1994, Pyle *et al.* 2001) makes these species excellent candidates for the use of archival tags, although they may be less tolerant of extra weight and/or drag than other species because their wings are adapted for underwater pursuit-diving and so flight is energetically expensive (Pennycuick 1987, Obrecht *et al.* 1988, Vandenabeele *et al.* 2012). Studies of small alcids have shown negative effects of tags ≤ 3% body mass

(Ackerman *et al.* 2004, Whidden *et al.* 2007, Elliott *et al.* 2010), and previous work on Crested Auklets (*A. cristatella*, one of the most highly migratory members of the genus) showed strong effects of a tag weighing 1% of body mass on several aspects of reproduction and behavior (Robinson and Jones 2014). In this study we investigated the effect of similar tags on the smaller, more resident Whiskered Auklet (*A. pygmaea*), and the larger, moderately migratory Parakeet Auklet (*A. psittacula*). The objectives of this study were (1) to measure the effects of tags on adult return rate and condition, reproductive success and chick growth rates, and (2) to evaluate the commonly accepted 3% guideline for tag mass in alcids in light of our data and a review of the literature. If there was a significant impact of tag attachment on auklets, we predicted reduced return rates of adults, reduced adult mass, reduced fledging success, and/or slower chick growth.

Methods

Literature Review

We reviewed 82 seabird tagging publications (including 65 tracking studies, and 17 that focused specifically on tag effects; see Appendix 2-1 for list of publications) for information about the size of device used relative to the size of the study species, how tag effects were measured/acknowledged, and, if measured, whether negative effects were found. This review included a broad range of device types and attachment techniques, and was intended to be a representative (but not comprehensive) sample of this kind of research.

Study site

This study was conducted 2012-2015, primarily at Buldir (52º 11' N, 175º 56' E), in the Aleutian Islands (part of the Alaska Maritime National Wildlife Refuge), where both species are relatively accessible due to the lack of native or introduced mammalian predators. Breeding crevices and burrows used were concentrated within and adjacent to US Fish & Wildlife Service long-term monitoring plots (see Knudtson and Byrd 1982, Byrd and Day 1986, Hipfner and Byrd 1993). We also tagged Parakeet Auklets at Gareloi Island (51º 47' N, 178º 47' W). These breeding sites were not monitored in detail and so the data are included for adult condition and return rate only.

Treatments

All breeding sites found were haphazardly assigned to treatments (see below), depending on visibility/accessibility of the bird within the crevice and estimated likelihood of recapture (*e.g.*, crevices with good visibility but possible escape routes were used for visual monitoring only).

Adult Tagged group: We tagged one or both members of the pair, returning every four to five days (when chicks were unattended) to measure chick growth and monitor nest fate (see below for details). This treatment was further differentiated for some analyses based on the type of tag (1 or 2g) and whether one or both members of the pair were tagged.

High-disturbance Control group: We removed and measured the adult, attached

an identification band only and recorded chick growth and nest fate, as in the Adult Tagged treatment.

Medium-disturbance Control group: An additional control for chick growth analysis in Parakeet Auklets only. We waited until the chicks were unattended and removed them for growth measurements; the adult was never handled.

Low-disturbance Control group: Visual monitoring of breeding site only; no capture of adults or chicks.

Device attachment

We attached 19 2g geolocation tags (LAT2900, 16 x 9 x 7mm, Lotek Wireless) on Parakeet Auklets (total attachment 3g, 1.1% body mass, mean 266g) in 2012. In 2013 we attached 23 1g tags (Intigeo C65, 14 x 8 x 6 mm, Migrate Technology) to Whiskered Auklets (total attachment 2g, 1.8% body mass, mean body mass 112g), 20 1g tags to Parakeet Auklets (0.8% body mass), and an additional 19 2g tags to Parakeet Auklets. The 2g tags were unreliable (7/11 initially recovered provided no usable data), so in 2014 we used 1g tags exclusively, deploying 69 on Parakeet Auklets and 25 on Whiskered Auklets (see Table 2-1 for detailed summary of sample sizes). We tagged adults as soon as possible after chicks hatched, because auklets are more prone to nest abandonment during the egg stage (Piatt *et al.* 1990, Ackerman *et al.* 2004), and breeding failure can increase the rate of divorce and/or crevice-switching the following year (Pyle *et al.*

2001), reducing the likelihood of recapture. One adult is usually present in the crevice at all times for a few days after hatch, allowing more reliable capture for tagging. When we missed that window, we returned to the crevice at night, when one or more adults are often still present throughout the breeding season (CRS, pers. obs.).

Birds were removed from the crevice and each given a numbered aluminum band crimped laterally to prevent slippage over the foot. Tagged adults were then given a custom-made Darvic color-band above the aluminum band upon which we attached LAT2900 tags by threading the band and a cable tie through metal loops on the tag. Intigeo C65 tags were attached to a Darvic band with a two part marine epoxy, further secured with a cable tie. For Parakeet Auklets, after a pilot study in 2012 showed that they were resilient to disturbance and able to tolerate the larger 2g tags, we began tagging both members of the breeding pair when possible to increase the sample size. Due to Whiskered Auklets' smaller size, and a lack of prior studies demonstrating tag tolerance, we tagged only one member of each pair to reduce the likelihood of significant effects on the chicks.

To evaluate the effects of the tags on adult condition, both tagged and control adults were weighed at the time of capture, and again at retrieval the following year. We also collected breast feathers for genetic sex determination (Fridolfsson and Ellegren 1999). If a tag was not retrieved one year after deployment, we continued checking that crevice in future years until the tag was recovered or the study ended. All crevices where birds had been previously captured were checked and individuals classified as either returned (the banded/tagged individual was recaptured or observed), or not returned (the

crevice was vacant, or confirmed to be occupied by new individuals). The fate of some birds was unclear because the status of one or more members of the pair could not be confirmed and we classified these individuals as not returned for the purposes of this analysis (including unclear returns as a separate category did not change the results). Our 'return rate' refers only to the rate of return to the same breeding crevice. Individuals that did not 'return' may have simply switched breeding sites and/or mates– a possible effect of the stress caused by carrying a geolocation tag (Jones and Montgomerie 1991, Fraser *et al.* 2004). However, every effort was made to search nearby crevices, and since most accessible crevices within our study areas are monitored, we believe we have maximized our chances of tag recovery.

Fledging success

To track the success of each nesting pair, we conducted regular crevice monitoring in the year of tag deployment, following US Fish & Wildlife Service protocols (Williams *et al.* 2000). This allowed us to compare our data to their large sample of monitored nests at Buldir as an additional 'low-disturbance' control. Briefly, this consists of visually inspecting crevices with a flashlight every 4-5 days, recording the presence of adult, egg, or chick, and determining the success or failure of each pair based on the age of the chick when last seen (Williams *et al.* 2000). For tagged and disturbed control sites (*i.e.*, high-disturbance and medium-disturbance controls), we also removed the chick during regular crevice checks and measured mass and flattened wing chord. Chicks were measured at approximately the same time of day, and masses were excluded if the chick had been recently fed (visually evident due to distended throat pouch). We calculated chick growth

rates (simple slope) for mass and wing during the linear growth phase (Parakeet Auklets: 4-22 days for wing, 10-31 days for mass; Hipfner and Byrd 1993; Whiskered Auklets: 7-26 days for wing, 2-22 days for mass; Hunter *et al.* 2002) for comparison among treatments.

Statistical analysis

All analyses were run in R v.3.1.1 (R Core Team 2014). Due to differences in the way the two species were tagged (different years, islands, treatment details), we analyzed each species separately. Some data points were excluded *a priori* from certain analyses (*e.g.*, two crevices destroyed in an earthquake were excluded from tests of return rates, and late hatching nests were excluded from tests of fledging success if their fate could not be determined). We used a generalized linear model (reporting deviance (*D*) and *P*-values from the χ^2 distribution; McCullagh and Nelder 1989) for binomial response variables (return rate and fledging success), with treatment, and year as fixed factors, and interactions between treatment and year. We also included island as a fixed factor for return rate of Parakeet Auklets, to account for possible differences between the Buldir and Gareloi colonies. Because sex was known only for manipulated nests, it was included as a factor in all return rate models, but in the case of fledging success we tested for the effect of sex (specifically the interaction between treatment and sex) separately using only individuals of known-sex, and excluded nests where both adults were tagged. We excluded 2014 Parakeet Auklet breeding sites from fledging success analysis because we left Buldir before the fate of the majority of successful nests could be determined. For

adult condition, we fit a general linear model on the difference between mass at deployment and mass at retrieval, with treatment, year, island (Parakeet Auklets only) and sex as fixed factors, and the difference in ordinal date between tagging and retrieval as a covariate to control for seasonal decline in mass (Weiser *et al.* 2016). For chick growth, we fit a general linear model with treatment (tagged, high-disturbance, medium-disturbance), year and sex as fixed factors, and the interaction of both year and sex with treatment. For Parakeet Auklets, the tagged adult category encompasses multiple treatments: nesting pairs had either a 1g tag, a 2g tag, or both members of the pair were tagged. These three categories were coded separately within the treatment factor for all initial analyses, with additional planned *a priori* comparisons (Sokal and Rohlf 2012) of: (1) all tagged adults *vs.* low-disturbance controls (fledging success only), (2) tagged adults with 1g *vs.* 2g tags (fledging success, chick growth), (3) breeding crevices with one *vs.* both adults tagged (fledging success, chick growth), and (4) all disturbed adults (adult tagged and high-disturbance control) *vs.* medium-disturbance controls (chick growth only). We also used a generalized linear model (binomial) to compare return rates of Parakeet Auklets bearing 2g tags with data from a study Crested Auklets using the same tags (Robinson and Jones 2014). We set an *a priori* significance level of $P < 0.05$ for all tests, and considered effects where $0.05 < P < 0.1$ to be of marginal significance and worth considering as a potential concern.

Results

Literature review

Among tracking studies reviewed (n=65), 52% made at least minimal measurements of effects, 11% made anecdotal statements that birds did not seem affected by tags, 6% cited previous research on their species, 8% cited the 3% guideline (Phillips *et al.* 2003) as evidence that measuring effects was not necessary, and 23% made no mention of effects. Of studies that measured effects (n=51), 41% reported some negative impact. The likelihood of detecting effects for tags 3-5% body mass was no higher than tags of 1-3% or <1% body mass (Table 2-2). We also found no tendency for small (<400g) species to have more negative effects than large (>1000g) species (Table 2-2). Taxonomy was the best predictor of tag effects in these publications. Fewer than 25% of studies on Procellariiformes or Laridae showed negative effects of tags, compared to 64% for Alcidae (Table 2-2).

Auklet tracking study

Overall we retrieved 79% of tags from Parakeet Auklets (deployed in 2012: 68%; 2013: 81%; 2014: 81%; see Table 2-1 for details), and 42% of tags from Whiskered Auklets (2013: 60%; 2014: 26%; Table 2-1). Control adult return rates were 70% for Parakeet Auklets (2012: 67%; 2013: 71%; Table 2-1) and 76% for Whiskered Auklets (2013: 67%; 2014: 100%; Table 2-1). One Parakeet Auklet had a leg injury of unknown origin that caused the tarsus to swell around the bands and bleed when they were removed. The bird was treated with a clotting agent and released back into the crevice, where it was observed incubating on subsequent visits. Several Whiskered Auklets showed evidence

of leg compression (*i.e.*, slight discoloration and indentation of the skin around the leg band) at the upper and lower joints of the tarsus due to the combined length of the aluminum and Darvic bands. This band crowding did not appear to impair leg function.

Parakeet Auklets: Treatment (Adult tagged 1g, Adult tagged 2g, High-disturbance control) had no effect on adult return rate ($D_{2,125}$=1.25, n=136, P=0.90) or condition (χ^2_2=3.03, n=90, P=0.22). In a comparison of Parakeet Auklets bearing 2g tags (1.1% body mass) with Crested Auklets given the same tags by Robinson and Jones (2014), we found that the two species responded differently despite their similar size (significant interactive effect of Species and Treatment: $D_{1,173}$=7.04, P=0.008). Tagged Crested Auklets had significantly lower return rates than controls (tagged 32% (10/31) *vs.* control 64% (83/129); $D_{1,127}$=29.9, P<0.001), while Parakeet Auklets did not (tagged 74% (28/38) *vs.* control 70% (7/10); $D_{1,46}$=0.05, P=0.82). There was a significant effect of year ($D_{1,103}$=15.0, n=105, P<0.001), but not treatment ($D_{4,99}$=3.52, n=105, P=0.47) on fledging success when all five categories (Adult tagged 1g, Adult tagged 2g, Adult tagged both, High-disturbance control, Low-disturbance control) were considered separately. Fledging success was lower in 2013 than 2012 (Fig. 2-1B). *A priori* follow-up tests showed no effect of treatment when comparing all tagged adults to low-disturbance controls ($D_{1,92}$=0.35, n=95, P=0.55), when comparing adults tagged with 1g and 2g tags ($D_{1,30}$=8.41, n=33, P=0.21), or when comparing nest crevices with one or both adults tagged ($D_{1,36}$=0.23, n=39, P=0.63). The final *a priori* test, comparing tagged adults to high-disturbance controls showed a marginal interactive effect of treatment and year on

fledging success ($D_{1,45}$=2.98, n=49, P=0.084), so the two years were analyzed separately. There was no difference between tagged and high-disturbance control treatments in 2012 ($D_{1,16}$=0.62, n=18, P=0.43). However, high-disturbance controls had higher fledging success than tagged adults in 2013 ($D_{1,29}$=4.6, n=31, P=0.032; Fig. 2-1B). When only birds of known sex were considered, there was a significant reduction in fledging success in tagged males (high-disturbance control 100%, 1g tag 67%, 2g tag 36%; $D_{2,14}$=8.32, n=18, P=0.02), but not females (high-disturbance control 67%, 1g tag 50%, 2g tag 80%; $D_{2,21}$=0.04, n=25, P=0.98). There was no significant effect of tagging on the rate that chicks increased in mass (average differences 1.23-3.30 g day^{-1}, $F_{4,37}$=1.20, n=45, P=0.33; Fig. 2-3B) or wing length (average differences 0.01-0.08 mm day^{-1}, $F_{2,41}$=0.34, P=0.72; Fig. 2-3A). Chick growth rates were significantly lower for both measures in 2013 than 2012 (average differences: mass 4.03 g day^{-1}, wing 0.40 mm day^{-1}, P<0.002; Figs. 2-3A - B).

Whiskered Auklets: There was a significant interactive effect of treatment and year on return rate ($D_{1,59}$=7.50, n=64, P=0.004), so each year was analyzed separately. There was no difference in return rate for tagged and control adults deployed in 2013 (65% *vs.* 67%; $D_{1,33}$=0.16, n=35, P=0.74), but tagged adults from 2014 had a dramatically lower return rate the following season (26% *vs.* 100%, $D_{1,27}$=12.9, n=29, P<0.001). Low recovery rates for Whiskered Auklet tags deployed 2014-2015 may be partially explained due to a delayed start to 2015 fieldwork. We arrived late in their incubation stage, and many crevices were vacant, but with downy feathers present suggesting that they had been occupied (and perhaps abandoned) before our first checks.

However, this would account for at most half of the missing tags. There was a marginally significant interactive effect of treatment and year on adult condition (X^2_1=3.68, n=64, *P*=0.055), so each year was analyzed separately. We found a significant difference in adult mass in 2013-2014 deployments (tagged adults returned on average 0.75g lighter than at deployment, control adults on average 5.8g heavier; X^2_1=11.7, n=22, *P*<0.001), but not in 2014-2015 (tagged adults returned on average 10.6g heavier than at deployment, control adults on average 10.3g heavier; n=12, *P*>0.9). Tagging treatment (adult tagged, high-disturbance control, or low-disturbance control) had no effect on Whiskered Auklet fledging success ($D_{2,175}$=1.38, n=179, *P*=0.50; Fig. 2-1A). There was also no effect of treatment (adult tagged or high-disturbance control; $D_{1,59}$=0.63, n=62, *P*=0.43) or interaction between treatment and sex ($D_{1,56}$=0.81, n=62, *P*=0.37) when only known-sex individuals were included. Tagging the adult significantly reduced the rate of mass gain in chicks (Fig. 2B; average difference 0.5 g day^{-1}, $F_{1,35}$=6.80, n= 41, *P*=0.01), but had no effect on wing growth ($F_{1,39}$=0.012, n=45, *P*=0.91; Fig. 2-2A). Chick growth was slower (although only marginally significant for wing) in 2013 than 2014, irrespective of tagging status (mass: average difference 0.38 g day^{-1}, $F_{1,35}$=3.08, n=41, *P*=0.02, Fig. 2-2B; wing: average difference 0.1 mm day^{-1}, $F_{1,39}$=3.53, n=45, *P*=0.07, Fig. 2-2A).

Discussion

Parakeet and Whiskered auklets showed varying tolerance for tags 0.8-1.8% body mass. There were minor decreases in chick growth for tagged Whiskered Auklets, suggesting that an increased burden reduced their ability to provision offspring, but not enough to

affect chick survival. We also found significant negative effects on adult condition and return rates of Whiskered Auklets in some years, but not in others. Low recovery rates for Whiskered Auklet tags deployed 2014-2015 may be partially due to a delayed start to 2015 fieldwork. However, many of the occupied crevices contained at least one new bird, suggesting high rates of mortality, divorce, or switching of breeding sites (Jones and Montgomerie 1991, Fraser *et al.* 2004, Paredes *et al.* 2005). The particularly harsh winter in the Bering Sea 2014-2015 may also have been a factor in the lower return rates. Whiskered Auklets remain resident in the Aleutians year-round (Byrd and Williams 1993), and survival has been shown to vary with local winter conditions, with higher mortality in stormy winters (Jones *et al.* 2007). The burden of tags may have exacerbated this effect, if individuals that could normally compensate were not able to do so when already operating near their metabolic limit (Croll and McLaren 1993, Costa 2007, Humphreys *et al.* 2007). Our data suggest that the tags used (total attachment: 2g) may have been too large for Whiskered Auklets to bear without experiencing considerable stress, and thus the tracking data produced should be interpreted with caution.

Parakeet Auklets, on the other hand, showed very few negative effects of tagging. In 2013 (a bad year for chick growth and survival overall) fledging success was lower for tagged birds than high-disturbance controls, but higher than the large sample of low-disturbance control nests monitored (Fig. 2-1B), and so the statistical difference may not be biologically meaningful. We also found that tagging of males was more likely to result in a negative effect on fledging success, suggesting that males may take on a greater share of the effort when provisioning the chick. Overall, though, Parakeet Auklets

showed a good tolerance for devices in this size range, with significantly higher return rates than Crested Auklets provided with the same 2g tags (Robinson and Jones 2014). Although closely related and similar in size, they differ in many ways, including the Parakeet Auklets' lower wing-loading, and shorter migration (Jones 1993, Jones *et al.* 2001), all of which likely contribute to their greater ability to carry the tags.

A review of seabird tagging studies illustrated the lack of consistency in reporting of tag effects in the literature. Among tracking studies, 52% made at least minimal measurements of effects, and of those, 41% reported some negative impact, although the statistical power of many studies was low due to limited comparative sample sizes and thus they were unlikely to detect anything but severe effects. Nevertheless, even a rudimentary examination of tag effects has value when it comes to interpreting the results of tracking studies, and researchers are urged to evaluate tag effects as a matter of standard practice (Vandenabeele *et al.* 2012). Lifestyle (as reflected by taxonomy) was the best predictor of tag effects in the publications reviewed (alcids were more than twice as likely to show negative effects of tags than other taxa; Table 2-2), suggesting that factors such as foraging style, or flight physiology/energetics may play a greater role than relative mass when predicting likely tag effects (Barron *et al.* 2010, Vandenabeele *et al.* 2012). Although relative tag mass alone was a poor predictor of tag effects (Table 2-2), studies testing multiple tag masses on the same species found that negative impact did increase with device size (*e.g.*, Wilson *et al.* 1986, Elliott *et al.* 2007, Ropert-Coudert *et al.* 2007), so percent body mass of tags deployed should be kept to a minimum.

Our study was not designed specifically to measure tag effects, but rather reflects the kind of data that can be gathered in the course of a larger tracking project, and we would encourage more researchers to incorporate at least minimal effects monitoring in all tracking studies. High rates of breeding failure (fewer active breeding sites to work with) at the colony in some years limited the size of our control samples (Table 2-1), and may have reduced our ability to detect more subtle tag effects, but having multiple years of data helps to make stronger conclusions. We have shown that effects can vary significantly among closely related species of similar size, and among years within the same species at the same colony. Given this variation, it is difficult to justify simply citing previous research when evaluating the potential for tag effects in any new study.

This study and others have demonstrated negative effects on reproduction, behavior, and return rates in alcids of tags well below the 3% guideline typically cited (*e.g.*, Ackerman *et al.* 2004, Paredes *et al.* 2005, Robinson and Jones 2014). These results suggest that not all species are equally affected by tags, and that guidelines, even those that are well-established for one group, should not be universally applied to all seabirds without validation (Vandenabeele *et al.* 2012). Temporal and geographic variation in tag effects within species (*e.g.*, this study, Weiser *et al.* 2016) also highlights the dangers of relying on previous effects studies, even of the same species. Factors other than tag mass may be at least as important. Most seabirds routinely carry food loads well in excess of 5% of their body mass (Ackerman *et al.* 2004, Ortega-Jimenez *et al.* 2011), and it has often been suggested that aerodynamic and/or hydrodynamic drag may be responsible for the increased energy costs at the root of many observed effects (Wilson *et al.* 1986,

Obrecht *et al.* 1988). Despite this, although nearly all tagging studies report gear mass, many fail to include tag dimensions.

Advances in light-weight tracking technology provide researchers with a powerful new source of data on seabird ecology during the non-breeding season. We can test hypotheses about migration behavior, map winter habitat to inform the design of marine protected areas, or answer other conservation questions. This information is valuable, but should, whenever possible, be reported alongside an assessment of tag effects. Depending on the duration of researcher presence and the accessibility of the site, many studies could incorporate a basic assessment of reproductive success and/or adult return rates relative to control birds with minimal additional effort and disturbance. Including effects studies in tracking projects would provide a measure of confidence for their interpretation, and allow us to weigh the value of the resulting data.

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Tables

Table 2-1. Parakeet and Whiskered Auklet samples sizes for each experimental treatment per year[a]

		2012	2013	2014
Parakeet Auklet	2g tags	13/19	15/19	n/a
	1g tags	n/a	12/16 (3/4)[b]	36/47 (15/22)[b]
	High-disturbance control[c]	2/3	5/7	n/a
	Medium-disturbance control[d]	10	3	n/a
	Low-disturbance control[e]	19	37	29
Whiskered Auklet	2g tags	n/a	n/a	n/a
	1g tags	n/a	12/23	6/25
	High-disturbance control[c]	n/a	10/15	6/6
	Medium-disturbance control[d]	n/a	n/a	n/a
	Low-disturbance control[e]	n/a	61	56

[a]For treatments involving recovery of adults the following year, numbers given as returned/deployed

[b]Sample sizes for Buldir Island, followed by sample sizes for Gareloi Island in parentheses

[c]Adults removed and measured, but not tagged. Chicks measured, and reproductive success monitored

[d]For Parakeet Auklets only: chicks measured and reproductive success monitored. No handling of adults

[e]Visual monitoring of reproductive success only

Table 2-2. Summary of studies included in review of tag effects, broken down by taxonomy, size of species studied, and percent body mass of tag used. Only studies that provided the relevant information were included, so totals may differ.

		Total number of studies reviewed	Number of tracking studies measuring tag effects[a]	Number of studies reporting negative effects[b]
Taxonomic group	Procellariiformes	32	11 (42%)	2 (12%)
	Laridae	8	4 (57%)	1 (20%)
	Alcidae	28	14 (74%)	16 (64%)
Adult body mass	<400g	19	11 (73%)	5 (33%)
	400-1000g	38	17 (59%)	11 (41%)
	>1000g	24	6 (30%)	6 (60%)
Percent body mass of tag	3-5% body mass	12	7 (70%)	4 (40%)
	1-3% body mass	43	17 (52%)	12 (44%)
	<1% body mass	24	9 (45%)	6 (46%)

[a] Not including studies focused specifically on tag effects

[b] Includes tracking studies that measured tag effects and studies focused specifically on tag effects

Figures

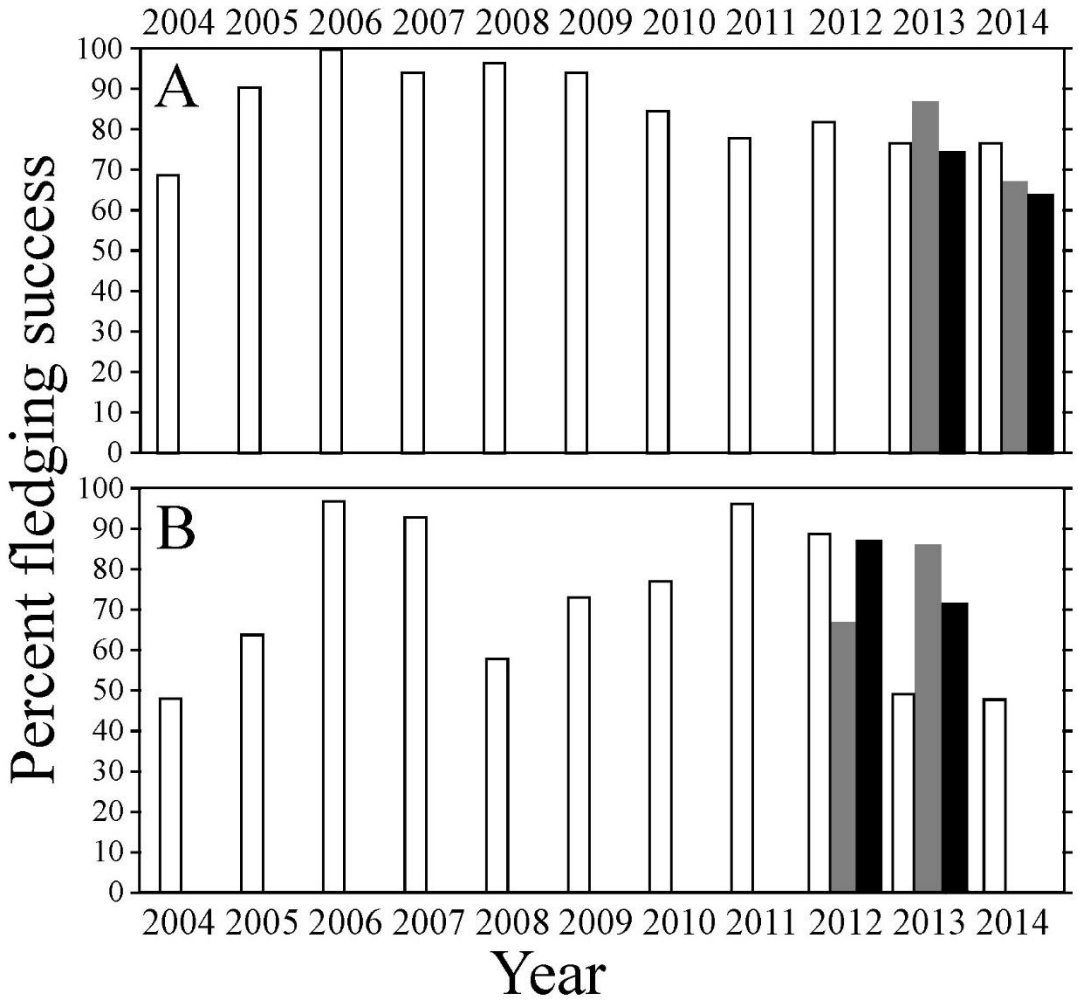

Figure 2-1. Fledging success of (A) Whiskered and (B) Parakeet auklets at Buldir Island, Alaska. Success of breeding crevices where adults were tagged with geolocators (black; all tag types combined) or had only leg bands attached (gray; high-disturbance control treatment). Long-term US Fish & Wildlife Service monitoring data (white; low disturbance; Mudge and Pietrzak 2015) included for context. Chicks from both the tagged and high-disturbance control treatments were captured and measured repeatedly to determine growth rates.

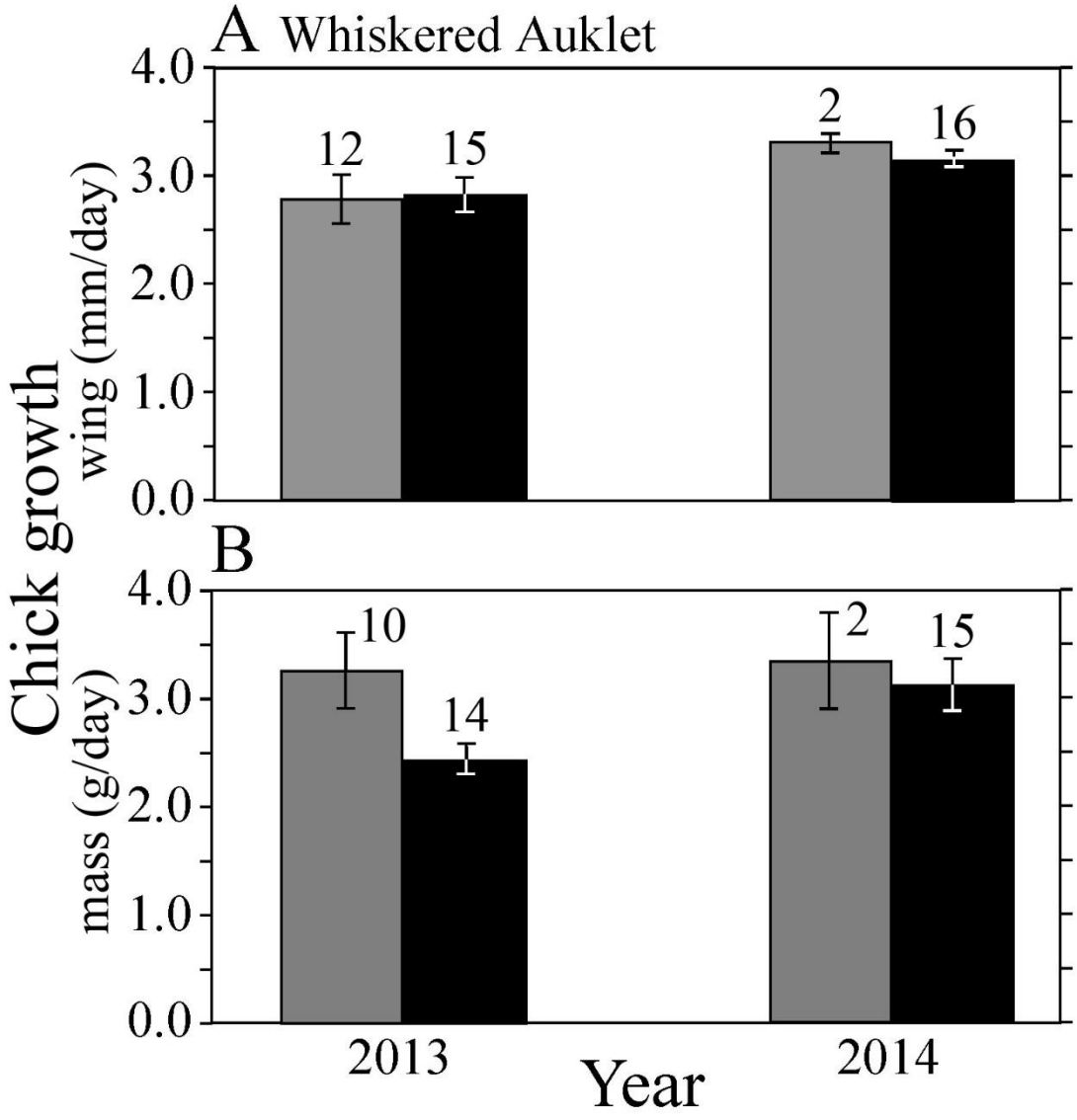

Figure 2-2. Growth rates of Whiskered Auklet chicks in wing length (A) and mass (B) during linear growth phase compared across treatments: High-disturbance control (gray), and Adult tagged (black). Sample sizes above bars. Note: we did not include a medium-disturbance control treatment (chick measurements only) for Whiskered Auklets, only Parakeet Auklets.

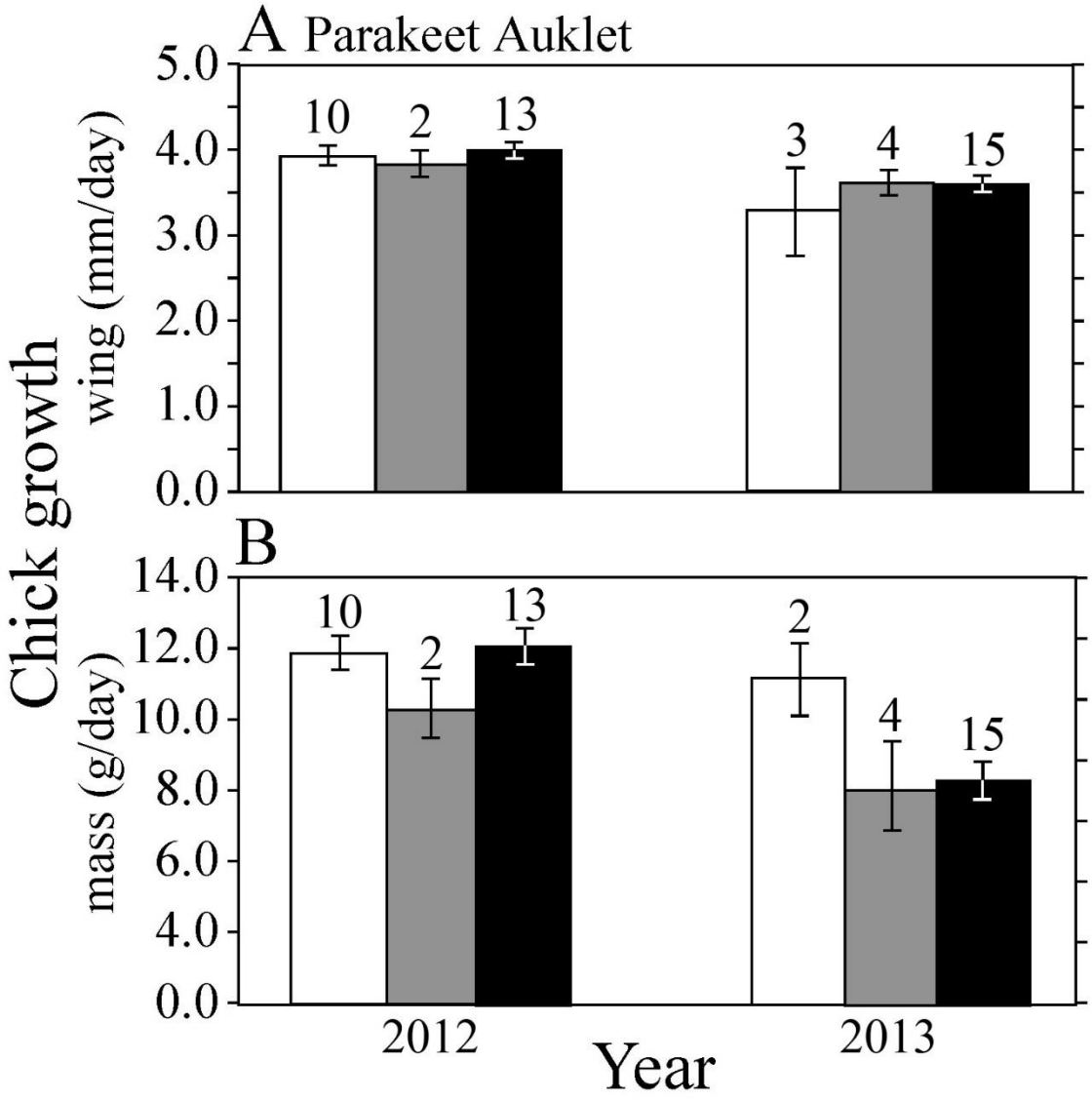

Figure 2-3. Growth rates of Parakeet Auklet chicks in wing length (A) and mass (B) during linear growth phase compared across treatments: Medium-disturbance control (white), High-disturbance control (gray), and Adult tagged (black). Sample sizes above bars.

CHAPTER 3: MIGRATORY TIMING IN COLONIAL SPECIES: IMPLICATIONS FOR POPULATION REGULATION

Abstract

Seabirds have a variety of migration strategies, but most derive ultimately from the fact that their feeding habitat at sea is unsuitable for reproduction. This produces a seasonal need to aggregate at breeding colonies, after which they are free to seek out preferred foraging habitat. Ashmole postulated that density-dependent regulation of seabird populations operates at the colony, likely involving decreases in local food availability ("Ashmole's Halo"). Studies have produced indirect data consistent with density-dependent effects on food availability for piscivorous seabirds, but the impact of competition at the colony and how that affects migration timing is unknown for planktivores. I compared three congeneric alcids (Whiskered Auklets, *Aethia pygmaea*; Parakeet Auklets, *A. psittacula*; Crested Auklets, *A. cristatella*) to test predictions derived from Ashmole's hypotheses and migration theory. I used tracking data for individuals with known breeding histories to compare lag between breeding cessation and onset of migration, and amount of synchrony within species and within breeding pairs. If food was a limiting factor, individuals should leave as soon as possible once breeding is completed, and species with higher metabolic demands (Whiskered Auklets) and/or greater potential impact on prey numbers due to large population and diet specificity (Crested Auklets) should be under greater pressure to leave. I found that Whiskered Auklets remained near the colony all year, and lag times for the other species were up to 30 days. Failed Crested Auklets stayed near the colony for weeks, while successful breeders left within a few days. Parakeet Auklets had long lag times regardless of nest fate, more variable departure dates, and more variable lag times for both successful and

failed breeders. Differences between Parakeet and Crested auklets were more consistent with differences in their migration strategies than with food availability. Crested Auklet departure timing was consistent with obligate migration, while Parakeet Auklet timing was consistent with facultative/dispersive migration.

Introduction

Migration has evolved in many taxa, usually as a strategy to survive in environments with a high degree of seasonality in resources (Boyle & Conway 2007, Dingle & Drake 2007, Shaw & Couzin 2013). Seasonal movements can take many forms, which may usefully be thought of as falling along a spectrum of migratory behaviours (Dingle & Drake 2007, Cagnacci *et al.* 2011). At one end of the spectrum is the traditional view of migration, with all individuals travelling from the breeding habitat to one or more distinct areas characterized by high winter productivity (*e.g.*, Dias *et al.* 2011, Hedd *et al.* 2012, Stenhouse *et al.* 2012). At the other end is year-round residence in the breeding area (*e.g.*, Ashmole 1962, Diamond 1975, McKnight *et al.* 2011). There are also intermediate strategies, such as dispersive migration, with individuals spreading out from the breeding site in many directions, or simply moving to different habitat in the general vicinity of the breeding site (*e.g.*, Harris *et al.* 2010, Hatch *et al.* 2010, Hedd *et al.* 2011).

Migrations can also be classified as obligate (individuals must migrate) or facultative (individuals 'choose' to migrate based on local conditions), although these are also more likely to be extremes on a continuum than a true dichotomy (Berthold 1975, Terrill 1990, Newton 2012). Obligate migrations (usually long-distance, directed migrations) are characterized by consistency in timing and destination among individuals

(Newton 2012). Departure from the breeding ground is preemptive, occurring before local conditions deteriorate, while food is still plentiful enough to build sufficient fuel stores for the journey (Berthold 1975, Terrill 1990, Newton 2012). Obligate migrations typically have a strong genetic component, with timing determined by an endogenous circannual rhythm, which can be adjusted based on external cues (such as photoperiod) that forecast future declines in local resources (Berthold 1975, Alerstam 1978, Terrill 1990). Facultative migrations (usually short-distance and/or dispersive) are more variable, and are under less rigid genetic control (Newton 2012). Departure is triggered directly by changes in local conditions (*e.g.,* food availability, temperature, weather; Terrill 1990, Newton 2012), with each bird responding according to their own internal threshold based on their individual condition, and energetic requirements (Chapman *et al.* 2011, Newton 2012).

Seabirds show great variety in migration strategy and the degree of flexibility in migration behaviours (Alerstam *et al.* 2003, Dingle & Drake 2007). The benefit of migration for these species derives ultimately from the fact that their typical feeding habitat at sea is unsuitable for reproduction, producing a seasonal need to aggregate at breeding colonies, usually in coastal areas or on remote oceanic islands (Ashmole 1971). Philip Ashmole (elaborating on the population regulation research of David Lack; 1954, 1966, 1968) postulated that any density-dependent effects regulating seabird populations must be operating at the colony, and most likely involve the availability of food, especially in tropical habitats that do not experience the seasonal increases in productivity seen at higher latitudes (Ashmole 1971). Specifically, Ashmole (1963) proposed that the

concentration of individuals with high nutritional needs (increased due to need to produce eggs, provision offspring, *etc*.) in a limited area will lead to a near-colony reduction in the availability of food ("Ashmole's Halo", Birt *et al.* 1987), either due to actual depletion of resources in the vicinity of the colonies, or interference competition from large numbers of foraging birds leading to decreased accessibility of prey. If so, the resulting increase in foraging effort required could serve as a proximate cue triggering post-breeding migration in some species.

Ashmole considered that his hypothesis was "almost unverifiable" (Ashmole 1971), but many have attempted to test it, with varying degrees of success. To my knowledge, only one study has shown direct evidence of reduced prey densities (of sedentary benthic fish) near seabird colonies (Birt *et al.* 1987). Other studies have addressed the question using indirect methods. Furness & Birkhead (1984) showed a negative relationship between colony size and the size of other nearby colonies, supporting the hypothesis of intraspecific competition near breeding sites. Modelling studies have also shown that it is theoretically possible for piscivorous seabirds to have a significant impact on the local food supply (*e.g.*, Wiens & Scott 1975, Furness & Cooper 1982). Other studies have shown density-dependent effects on reproduction (Hunt *et al.* 1986) and population growth rates (Lewis *et al.* 2001), which were attributed to increased interference competition near the colonies. In recent years the use of tracking tags and other data recorders has allowed investigation of the foraging behavior of individuals, showing that birds from larger colonies travel farther to forage (Ainley *et al.* 2003, Gaston *et al.* 2013, Oppel *et al.* 2015), and that birds foraging farther from the colony

bring back better prey, with foraging distances increasing over the course of the breeding season (Elliot *et al.* 2009).

The studies discussed above focused on piscivorous seabirds. The impact of competition at the colony is unknown for planktivorous species, especially in rich temperate areas where the breeding season for most species is expected to be timed to take maximum advantage of seasonal increases in productivity (Ashmole 1963, 1971). There is some evidence that large colonies of planktivorous Cassin's Auklets and Ancient Murrelets are spaced further apart than small colonies, although most (but not all) of the spatial bias can be explained by the constraint of island size (Forbes *et al.* 2000). The lateral distribution of zooplankton, unlike most fish species, is determined mainly by passive transport, and concentration by features of the local oceanography (currents, fronts, upwelling, *etc*.; Mackas *et al.* 1985). Calculations have shown that input of prey into the waters around a colony (advective resupply) matches or exceeds caloric demands based on seabird numbers and size (Bourne 1983, Schneider *et al.* 1992). In fact, the distribution of large seabird colonies around the world can often be explained by the proximity of productive currents (*e.g.*, Wilson-Merrill 2005, Sandvik *et al.* 2016). Springer *et al.* (1996) reviewed evidence for what they called the "Bering Sea Green Belt" (see also Piatt & Springer 2003), a system of currents transporting nutrients and plankton from the productive shelf break area into the northern shelf habitat and the Chukchi Sea, an important foraging area for many seabird species (Gall *et al.* 2013, Kuletz *et al.* 2015) until the expanding pack ice drives them further south. The Bering Sea remains a productive area year-round for species that can tolerate harsh and stormy

conditions, primarily due to an abundance of oceanographic features that serve to concentrate zooplankton near the surface (Springer *et al.* 1996, Hunt 1997, Ladd *et al.* 2005), even during autumn and winter when most zooplankton undertake a seasonal migration to greater depths (Conover 1988, Kobari and Ikeda 1999). Winter seabird abundances are especially high along the shelf break and in narrow Aleutian passes, where strong currents and localized upwelling provide reliable concentrations of accessible zooplankton (Schneider et al 1987, Springer *et al.* 1996, Ladd *et al.* 2005, Suryan *et al.* 2006). The question remains, if the Bering Sea is such a productive wintering area, why do seabirds breeding in the area migrate? Birds from the northernmost colonies must move south to avoid the encroaching ice, but most have no such constraint. Migration movements come with substantial energy costs (Alerstam *et al.* 2003), especially for alcids, whose wings are adapted for pursuit-diving, making flight energetically expensive (Pennycuick 1987, Gaston & Jones 1998, Elliot *et al.* 2013). Therefore, migration should only be favoured if the benefits outweigh those costs.

Aethia auklets breeding in the Aleutian Islands of Alaska (Fig. 3-1) provide an excellent system for the study of migration in light of Ashmole's hypotheses. They are small, cold-water seabirds with high metabolic demands (Johnson & West 1975), creating strong selection pressure to locate and exploit the most abundant and reliable sources of prey. With wing shapes adapted for pursuit-diving, both flight and foraging are energetically costly (Pennycuick 1975, 1987, Elliot *et al.* 2013), making them more dependent on foraging hotspots with high productivity and predictable distributions of prey (Schneider *et al.* 1986, Wahl *et al.* 1989). Despite these commonalities, the three

species studied here differ in several important ways. Differences in size translate into differences in metabolic requirements (see calculations below). They also differ in physiology and behaviour. Whiskered Auklets are nocturnal (in this part of their range), and feed in tide rips within 16 km of shore (Byrd & Gibson 1980). They breed at many small colonies throughout the Aleutians (Byrd *et al.* 2005), and remain near the islands year-round (Byrd & Williams 1993, NPPSD 2015), with anecdotal evidence suggesting that they return to the colony site during the winter (Stejneger 1885, Murie 1936, 1959, Dick & Donaldson 1978, Zubakin & Konyukhov 2001). As the smallest species in this study, they also should have the highest relative food requirements (101% of their body mass/day, compared to 79% for Crested and Parakeet auklets; Schneider *et al.* 1986, Birt-Friesen *et al.* 1989). Crested Auklets breed at much higher densities (Byrd *et al.* 2005), and are gregarious, engaging in conspicuous social behaviour on the surface of the colony. They also leave (and return to) the colony in large flocks to forage offshore (Bédard 1969, Gaston & Jones 1998). Compared to most alcids, their wings are relatively narrow and streamlined (characteristic of migratory species, Mönkönnen 1995; aspect ratio 8.4 +/- 0.7 SD, Chapter 5; Gaston & Jones 1998), allowing for faster, more energy-efficient flight (Rayner 1990). Their summer diet is specialized, dominated by euphausiids and calanoid copepods (Hunt *et al.* 1998, Guy *et al.* 2009, Bond *et al.* 2011). The limited data available suggest that their winter diet may be more varied (Bédard 1969, Troy & Bradstreet 1991), but much remains unknown. Preliminary data from tracking studies suggest that Crested Auklets undertake a long-distance, directed migration, with a high degree of consistency in wintering areas (Robinson 2015, K.F.

Robbins, unpublished data). Parakeet Auklets breed at much lower densities (Byrd *et al.* 2005), and are less gregarious, flying out to forage singly or in small groups (Gaston & Jones 1998). Although similar in size to Crested Auklets, they have a broader wing (lower aspect ratio: 7.6 +/- 0.3 SD; Chapter 5). Parakeet Auklets also have a more generalist diet, including mollusks, gelatinous zooplankton, euphausiids, copepods, and larval fish (Day & Byrd 1989, Harrison 1990, Hunt *et al.* 1998), and preliminary data suggest a more dispersive migration (discussed in more detail in Chapter 5). Differences in gregariousness between Parakeet and Crested Auklets likely continue into the non-breeding season. Much larger winter flock sizes were observed for Crested than Parakeet auklets during ship-based surveys (Crested Auklet average flock size 32 +/- 232, maximum 10,500; Parakeet Auklet average 3 +/- 8, maximum 213, NPPSD 2015; Gaston & Jones 1998).

To investigate how these species differ in their response to being released from the constraint of remaining near the colony, I combined monitoring of individual reproductive timing (specifically the date at which the current breeding season was completed by the death or successful fledging of the offspring) with tracking data obtained from geolocation tags deployed on those same individuals (to determine the date of departure from the colony). The objectives for this study were to: (1) determine the timing of migration in relation to the cessation of breeding in three closely related alcid species, (2) determine the amount of synchrony in migration within species and within breeding pairs, and (3) use these data to test predictions derived from Ashmole's hypotheses and migration theory. If food is an important limiting factor at the colony

(either due to food depletion, or interference competition), I would expect individuals of all species to leave as soon as possible once released from the need to return to the colony to incubate/provision their offspring. If individuals leave quickly after breeding, I would also expect both members of a breeding pair to leave at approximately the same time. Species with the highest metabolic demands (*i.e.,* Whiskered Auklets) should be under the most pressure to seek out better food sources away from the colony, and species with a greater potential to impact their food supply (*i.e.,* Crested Auklets breeding at higher densities with a more specific diet) should benefit more by leaving than generalist feeders breeding at lower densities (*i.e.,* Parakeet Auklets). I also predict that, given their more directed, long-distance migration (K.F. Robbins unpublished data), Crested Auklet departure patterns will be more consistent with obligate migration (greater degree of synchrony and consistency in timing) than those of the more dispersive Parakeet Auklets.

Methods

Study area

This study was conducted at Buldir (Fig. 3-1; estimated population of 30000 Whiskered, 280000 Crested, and 12000 Parakeet auklets, Byrd *et al.* 2005) and Gareloi (Fig. 3-1; estimated population of 186000 Crested and 43200 Parakeet auklets, Byrd *et al.* 2005) islands in the western Aleutian Islands, a part of the Alaska Maritime National Wildlife Refuge. Breeding sites (crevices and burrows) used on Buldir were concentrated at Main Talus (Whiskered and Crested auklets; 52°22’N, 175°54’E), Bottle Hill (Parakeet Auklets; 52°20’N, 175°56’E), and Northwest Ridge (Whiskered and Parakeet auklets; 52°22’N, 175°52’E), with additional sites located along the rocky cliffs of the northern

shore (see descriptions in Knudtson and Byrd 1982, Hipfner and Byrd 1993, Jones *et al.* 2001). These sites were spread across a variety of habitats (*e.g.*, rocky talus slopes, vegetated hillsides) representative of most auklets breeding at Buldir. On Gareloi I tagged Crested Auklets in semi-vegetated crevices in a lava flow on the southeast coast (51°45'N, 178°45W), and Parakeet Auklets breeding on a grassy hillside (51°46'N, 178°44'W) similar to the Northwest Ridge habitat on Buldir.

Device attachment and productivity monitoring

I used a 1g light-based archival geolocation tag (Intigeo C65, 14 x 8 x 6 mm, Migrate Technology) for all species (total attachment 2g, 1.8% body mass for Whiskered Auklets, 0.8% for Parakeet and Crested auklets). I tagged adults as soon as possible after the chick hatched to minimize the likelihood of nest abandonment (Piatt *et al.* 1990, Ackerman *et al.* 2004) and maximize tag recoveries the following year.

I removed birds from the crevice by hand, or by using a long, blunt metal hook placed around the tarsus/tibia. I gave each adult a numbered aluminum band crimped laterally to prevent slippage over the foot, and a custom-made Darvic colour-band with a flattened side to which tags were attached with a two-part marine epoxy and secured with a cable tie. I also collected breast feathers for genetic sex determination (Fridolfsson and Ellegren 1999) at the Genomics and Proteomics Facility at Memorial University of Newfoundland. Preliminary data showed that Parakeet Auklets were resilient to disturbance and suffered minimal negative effects from tagging (Chapter 2), so for Parakeet (and, to a lesser extent, Crested) Auklets, I tagged both members of the breeding pair, when possible, to investigate the amount of synchrony in migration timing within

pairs. Due to Whiskered Auklets' smaller size, and a lack of prior studies demonstrating tag tolerance, I tagged only one member of each pair to reduce the risk of significant effects on the chick.

To track the productivity of each bird, I conducted regular crevice monitoring at Buldir Island following US Fish & Wildlife Service protocols (Williams *et al.* 2000). Briefly, I visually inspected crevices with a flashlight every 3-4 days, recording the presence of adult, egg, or chick, and determined the fledging success of each pair based on the age of the chick when last seen (Williams *et al.* 2000). I defined the breeding cessation date as the midpoint between the last day the egg/chick was seen alive and the first day the egg/chick was recorded dead/absent. In the case of eggs that failed to hatch, I considered the breeding attempt abandoned when an adult was no longer present in the crevice to incubate during the day. If the chick was still present at our last monitoring visit, but was old enough to assume successful fledging (using species-specific criteria in Williams *et al.* 2000), I estimated the fledging date by adding the average age at fledging during the study period (Whiskered Auklets: 39 days, Parakeet Auklets: 32 days, Crested Auklets: 36 days) to the hatch date. If that estimate was earlier than the last known date that the chick was present, I used the day after the final sighting. Nests were excluded if the chick was too young at last sighting to assume successful fledging, or if either hatch or disappearance date could not be determined within 3-4 days (*e.g.*, if the interval between checks was >7 days, or if I could not visualize the egg/chick during the hatching/fledging period). Limited researcher presence meant that nest monitoring was more sporadic at Gareloi Island (especially for Parakeet Auklets, due to the remoteness of

the breeding sites), so many Gareloi birds did not meet the above criteria and were excluded from breeding cessation date analyses.

Tracking data processing

I deployed 5 tags for 13 days in June 2014 on a hilltop near the colony as an open-sky calibration to determine an appropriate elevation angle for this region to use as a parameter when estimating location from the sunrise/sunset data recorded by the tags (Lisovski *et al.* 2012). The resulting elevation angle (-5.6, threshold = 2) was evaluated for each bird using breeding season data (birds known to be at/near the colony), and was found to be acceptable in most cases. For a few individuals this angle resulted in a distribution of points that did not overlap with the island at all (skewed too far south), and in these cases I shifted the angle until the breeding season data overlapped with the known location of the birds. I also deployed 5 tags year-round at a known location on Buldir Island as a control to evaluate the accuracy of the tags. Data from these tags were processed in the same way as the bird-borne tags.

I used IntiProc (Migrate Technology Ltd) software (based on the GeoLight 2.0 R package; Lisovski & Hahn 2012) to process the raw light curves provided by the geolocation tags. I scored each sunrise/sunset event according to the quality of the light curve, based on the amount of shading evident. I then mapped the individual points. Obvious outliers that were also associated with a low score due to tag shading were removed, as were latitudes for points near the equinoxes (9 Sept - 18 Oct, 24 Feb - 4 Apr for Parakeet and Whiskered auklets; 9 Sept - 14 Oct, 27 Feb - 3 Apr for Crested Auklets) when day lengths around the planet are too similar for reliable estimates of latitude (Hill

& Braun 2001). I smoothed the data twice (Phillips *et al.* 2004), using a 3 day running average, with fixed origin points at the beginning and end of each track and of equinox exclusion periods (Hedd *et al.* 2012). I plotted the latitude and longitude over time for each individual (see Fig. 3-2 – 3-4 for a representative example from each species) to determine the date at which they left the colony vicinity, as represented by a clear, directional movement away from the area. Individuals were excluded if gaps in the tracking data occurred at the time of departure (*e.g.*, increased cloud-shading due to stretches of poor weather can result in a large number of erroneous points being filtered out during processing).

Analysis

To quantify the time between cessation of breeding and onset of migration (hereafter 'lag'), I subtracted the Julian breeding cessation date from the departure date. I tested for differences between species in departure date and lag by fitting general linear models with factors for species, nest fate (successful fledging of chick, or failure due to abandonment or death of offspring), sex of tagged adult, year of tagging and island, and the interactive effects of species and fate. I also performed one-sided t-tests to determine if lag was significantly greater than zero. To test how departure date related to breeding cessation date for different species, I performed an ANCOVA (with interactive effects of species and breeding cessation date). I compared departure dates within breeding pairs using a paired t-test. Models were evaluated using residual *vs.* fit plots and histograms of residuals to validate the assumption of straight-line regression models (breeding cessation

vs. departure date) and normal error models for computing p-values. Results are presented as mean +/- standard deviation (SD), unless otherwise noted.

Results

In 2014 I found that adult Parakeet Auklets whose breeding attempt had already failed could often be found in their breeding crevices at night. I did not do a systematic survey of this phenomenon, since I was only looking for individuals that had not already been tagged during our regular daily checks, but I did find six birds in crevices at night 5-38 days after the egg was considered abandoned (no longer incubated during the day). In three of those cases the egg was broken or absent. There was also one crevice where both members of the pair were present together at night 16 days after their chick was found dead, and one crevice where the adult was found at night despite being inactive that year (there was never an egg in the crevice). That individual was recaptured the following year in the same crevice, and so was unlikely to have been breeding elsewhere in the colony.

I obtained 17 year-round tracks for Whiskered Auklets, 64 for Parakeet Auklets (includes two individuals with 2 years of data), and 98 for Crested Auklets (includes two individuals with 2 years of data; see Table 3-1 for detailed breakdown of sample sizes).

Whiskered Auklets remained in the vicinity of the colony all year (*e.g.*, Fig. 3-2). The average distance between recorded Whiskered Auklet locations and the colony site was 212 km (coefficient of variation CV=0.88, n=8049) from the colony (199 km in latitude, CV=0.95, n=8049; 49 km in longitude, CV=0.99, n=8049), which was greater than the average error in calculated locations for stationary calibration tags deployed

year-round at a known location on Buldir Island (120 km, CV=0.96, n=2217), but within the margin of error for similar tags when deployed on birds (169-400 km reported in other studies; Phillips *et al.* 2004, Shaffer *et al.* 2005). Because there were no departure dates for Whiskered Auklets, I proceeded with the rest of the analysis using Parakeet and Crested auklet data only.

Departure date depended on species ($F_{1,73}$=4.67, p=0.03; Fig. 3-5), and nest fate ($F_{1,73}$=39.75, p<0.001; Fig. 3-5). Average date of departure was almost identical in both species (Julian date 215-216, August 3-4), but there was higher variance ($F_{63,72}$=2.51, p<0.001; Fig. 3-5) for Parakeet Auklets (215.7 +/- 10.4 days) than Crested Auklets (214.8 +/- 6.6 days). In both species, failed breeders (207.2 +/- 8.8 days) left earlier than successful breeders (218.0 +/- 5.0 days), with an average difference of 15.0 days for Parakeet Auklets, and 11.3 days for Crested Auklets. Departure date depended on breeding cessation date ($F_{1,70}$=79.75, p<0.001; R^2=0.53; Fig. 3-6), but there was considerable spread above the 1:1 line (Fig.3- 6), depicting delayed departure, and the relationship was tighter for individuals with later breeding cessation dates (mostly successful nesters) than for early failures. The 95% confidence limits (CL) for the overall slope of the regression of departure date on breeding cessation date (0.59 days/day after breeding cessation, CL 0.39-0.79) exclude a 1:1 relationship, indicating reduction in lag time later in the season. When the two species were analyzed separately, the 95% confidence limits for the slope excluded a 1:1 relationship for Crested Auklets (slope 0.59 days/day after breeding cessation, CL 0.43-0.75; R^2=0.55), but not for Parakeet Auklets (slope 0.72 days/day after breeding cessation, CL 0.43-1.01; R^2=0.50). I obtained

simultaneous tracking data for 20 Parakeet Auklet breeding pairs, and 3 Crested Auklet pairs. There was no significant difference in departure dates between members of the same breeding pair (average difference 4.2 +/- 3.9 days, range 0-13 days; paired t-test; t_{22}=0.39, p=0.70; Fig. 3-7). Removing the 3 Crested Auklet pairs from the analysis did not change the results (average difference 4.3 +/- 4.1 days; t_{19}=0.07, p=0.94).

One-sided t-tests showed that lag for both species was greater than 0 days (range: -3-30 days; t_{73}=10.00, p=0<0.001). Lag differed significantly depending on species ($F_{1,64}$=900.09, p<0.001; Fig. 3-8) and nest fate ($F_{1,64}$=549.59, p<0.001; Fig. 3-8). Failed breeders of both species stayed on average 14 days after breeding cessation (Parakeet Auklets: 14.0 +/- 8.7 days; Crested Auklets: 14.1 +/- 8.8 days; Fig. 3-8). Successful Parakeet Auklet breeders stayed 2.7 times longer than successful Crested Auklets (Parakeet Auklets: 11.2 +/- 5.0 days; Crested Auklets: 4.2 +/- 2.8 days; Fig. 3-8), and had higher variance ($F_{5,36}$=3.07, p=0.04; Fig. 3-8). Failed Crested Auklet breeders had higher variance in lag than successful Crested Auklets ($F_{8,37}$=9.81, p<0.001; Fig. 3-8), but that was not the case for Parakeet Auklets ($F_{19,5}$=3.06, p=0.22; Fig. 8).

Discussion

I predicted that if food was an important limiting factor at these auklet colonies (due to food depletion or interference competition), individuals should leave as soon as possible once no longer tied to the colony by their offspring. My data did not support this prediction. Whiskered Auklets (which, with the highest metabolic demands, should have been under the most pressure to seek out the best food sources) did not migrate at all. Instead, they remained resident at or near the colony all winter (discussed in more detail

in Chapter 4). The migratory Parakeet and Crested auklets did not leave as soon as breeding was completed. Failed breeders of both species left earlier than successful breeders, but still had long lag times (up to 30 days, overall average 9 days) after cessation of breeding. Both members of a breeding pair left at approximately the same time (at least for Parakeet Auklets; with only three Crested Auklet pairs I do not have enough data to make a strong conclusion for that species). However, since most individuals did not leave quickly after breeding, it is possible that this synchrony within pairs is the result of individuals with similar breeding experiences requiring a similar amount of time to prepare for migration.

My results are consistent with existing preliminary data placing these three closely related species at different points on the spectrum of migration behaviour, ranging from year-round residence in the Whiskered Auklet, to facultative/dispersive migration in the Parakeet Auklet, to obligate/directed migration in the Crested Auklet. Winter residence at the breeding site is uncommon in seabirds (Bridge 2006), but it could be energetically favorable to remain near the colony if sufficient prey is available to sustain the population over winter. Whiskered Auklets specialize in feeding at local tide rips close to the island (Byrd & Gibson 1980, Herter 1991, Byrd & Williams 1993), which operate year-round to provide an accessible source of food near the surface (Holm & Burger 2002, Ladd *et al.* 2005). The limited data available on winter diet in this species suggest that Whiskered Auklets in the western Bering Sea (Bering Island) switch from the copepods preferred during the breeding season (Day & Byrd 1989) to eating mainly gammarid amphipods (Stejneger 1885), which do not provide enough nutritional content to successfully raise

chicks (Bédard 1969), but may be sufficient during the non-breeding season when energetic demands are reduced. In the eastern Aleutian Islands (Unimak Pass), euphausiids dominate winter diet (Troy & Bradstreet 1991). Whiskered Auklets breed at low densities, so the local resources available around Buldir Island in winter may be able to support the small population of Whiskered Auklets (~30000) even if they would not be sufficient to feed hundreds of thousands of Crested Auklets. There are also data to suggest that Whiskered Auklets are able to further reduce their energetic requirements during the winter by roosting on land and avoiding the metabolic costs of resting in cold water at night (see Chapter 4). It is unknown if Whiskered Auklets at other colonies exhibit the same residence behaviour, although it seems likely for most colonies (*e.g.*, Aleutian and Kuril islands) that are not surrounded by pack ice in winter (Gaston & Jones 1998).

Parakeet and Crested auklets differed in the timing of their departure from the colony (Figs. 3-5, 3-8). Failed Crested Auklets (earlier breeding cessation dates) stayed at/or near the colony for weeks, while successful breeders generally left within a few days and showed less variation than failed breeders (Fig. 3-8). Parakeet Auklets, on the other hand, had long lag times regardless of nest fate, and showed less evidence than Crested Auklets of a decrease in lag over the course of the season (Figs. 3-6, 3-8). They also had more variable departure dates and more variable lag times for both successful and failed breeders (Figs. 3-5, 3-8). These results are consistent with a more highly synchronized departure in Crested Auklets, characteristic of obligate migration, in which migration movements are pre-emptive of seasonal changes in local conditions (Dingle & Drake

2007, Newton 2012). The tighter distribution of departure dates over time (Fig. 3-6; Alerstam 1978) suggests that there is an optimal window of departure late in the breeding season. Preliminary data showed that most Crested Auklets from these colonies made an initial trip north to the northern Bering and/or Chukchi seas, feeding there until the advancement of the ice pushed them south to their secondary wintering area (Robinson 2015, K.F. Robbins unpublished data). The 'migration window' inferred from departure patterns could be produced if departure dates are under selection to maximize exploitation of this productive seasonal habitat during the limited time available. Crested Auklets are also highly gregarious, and when departing the colony for daily foraging trips they wait until a large number of individuals are ready, and fly out to sea in large flocks (Jones 1993).They are observed wintering at sea in similarly large groups (Troy & Bradstreet 1991, NPPSD 2015), and it is likely that they undertake their migration departure in the same way (IL Jones, pers. comm.). Individuals failing early in the season may linger at the colony building energy reserves for the flight and waiting for a sufficient number of birds ready to depart, while successful breeders finishing late in the season are more synchronized and have less time to prepare before the 'migration window' closes. A similar pattern was found in spring songbird migrations where later birds were more synchronous than early ones during the spring migration (when there are competitive advantages to early arrival at the breeding grounds; Hagan *et al.* 1991), and in autumn migrations where early migrants will wait at stopover sites for a window of good weather, while later birds will continue through all but severe weather (Alerstam *et al.* 1978).

The lower synchrony in Parakeet Auklets is consistent with a more facultative/dispersive migration (Newton 2012), with little evidence of a strong internal clock regulating departure times, or pressure for a rapid departure from the colony. Although some individuals undertook the same initial northward migration to the ice edge as Crested Auklets (Kuletz *et al.* 2015, Chapter 5), the majority did not, and instead moved shorter distances to a variety of destinations within the Bering Sea, with some returning to the vicinity of the colony periodically throughout the winter (Chapter 5). Parakeet Auklets not only remained near the island long after breeding failure, some returned to their breeding crevices at night. There may be a territorial advantage to this behaviour if it allows them to defend the site from potential competitors (*e.g.*, sub-adults that spend the breeding season prospecting for future breeding attempts; Kokko *et al.* 2004). Remaining at the colony may also serve a social function. Parakeet Auklets do not engage in the same conspicuous social displays as Crested Auklets, but they are active on the surface of the colony and in the breeding crevices at night and early in the morning (CRS pers. obs.). These appear to be the periods when the majority of pairs switch incubation shifts; I often found both members of the pair vocalizing together in the crevice at night. Alternatively, they may simply return to the crevice at night for shelter and to avoid the metabolic costs associated with resting in cold water until they eventually leave the vicinity of the colony (see discussion of similar behaviour in Whiskered Auklets; Chapter 4).

Geolocation tags have low precision (range of error 169-400 km when deployed on birds; Phillips *et al.* 2004, Shaffer *et al.* 2005) relative to other types of tracking tags

(Wakefield *et al.* 2009). This limits my ability to detect small-scale movements, and prevents me from making a more detailed analysis of post-breeding behaviour in these species. However, the large-scale directed movements away from the colony (migration departure) of interest for this study are clearly apparent in the data. Studies of tagged birds also involve the assumption (explicit or implied) that the behaviour measured in tagged birds is representative of the behaviour of 'normal', undisturbed individuals. To validate this assumption, my collaborators and I performed an experimental evaluation of tag effects alongside this study (Chapter 2, Schacter & Jones 2017, K.F. Robbins unpublished data). We found little or no effect of 1g tags on Parakeet and Crested auklets, but there were significant reductions in chick growth and adult return rate for Whiskered Auklets, and so those results must be interpreted with caution. However, the lack of migration observed in Whiskered Auklets was consistent with previous anecdotal evidence and ship-based surveys (Murie 1936, Zubakin & Konyukhov 2001, NPPSD 2015), so I believe that my conclusions for Whiskered Auklets are well-supported (see more detailed discussion of Whiskered Auklet wintering behavior in Chapter 4).

I found no evidence that competition for food at the colony (direct or indirect) was an important factor for these planktivorous seabirds. Early failed breeders left before later breeders, but not as soon as possible. Some lag is to be expected while the birds feed and build up their condition before migration, and does not necessarily rule out food depletion or interference competition near the colony. However, if early failed breeders were remaining to build up reserves, I would expect late failed breeders to do the same. I would also expect late finishers to require more time to recover their condition than early

finishers, not less, having invested more time and energy in the reproductive attempt. My results were inconsistent with this interpretation for auklets. In contrast, a tracking study of Black-browed Albatrosses showed that birds that failed early in the season departed for their winter feeding grounds in the Benguela upwelling zone months before late failures and successful birds (Phillips *et al.* 2005), suggesting that prey depletion may have been a factor at that colony, or at least that there was a large advantage in relocating to the highly productive wintering area as soon as possible. In the case of the auklet colonies, it is more likely that the local current systems are providing a reliable influx of planktonic prey (advective resupply; Bourne 1983, Schneider *et al.* 1992). More studies of this nature will be needed to determine if there are consistent differences among planktivorous and piscivorous species.

Given my results, it is unlikely that reduced food availability acts as a proximate trigger of migration in this system. As facultative/dispersive migrants, Parakeet Auklets should be more responsive to local cues (*i.e.,* more likely to leave due to declining food availability; Newton 2012) than Crested Auklets, not less as suggested by my data. I speculate that migration timing in these species has more to do with conditions at the wintering area than those at the breeding site. Crested Auklets, with their large flock sizes and high diet specificity should be under stronger selection pressure to seek out and exploit the most abundant and reliable sources of food, in this case the productive Chukchi Sea. The more generalist, less gregarious Parakeet Auklets can afford to be more flexible in the timing (and destination) of their migration, following no pre-determined

route and making individual decisions based on their current condition and changes in the local environment.

The different migration strategies employed by these species also suggest different conservation concerns. The year-round residence of Whiskered Auklets at the breeding site has already made them more vulnerable to introduced mammalian predators (Williams *et al.* 2003). The flexible, generalist strategy of Parakeet Auklets likely makes them more adaptable to environmental changes than Crested Auklets, whose less flexible migration schedule, combined with their reliance on northern habitat could make them vulnerable to climatic changes affecting the timing and/or extent of the Arctic ice pack. However, annual variation in the number of Crested Auklets observed in the Chukchi Sea (Gall *et al.* 2013) suggests that there may be more flexibility in later stages of the migration than in the initial departure from the colony. This system provides an interesting opportunity to study three closely related species on different parts of the migration spectrum. Future work will focus on confirming our classification of these species using other aspects of the migration journey, such as duration, use of stopovers, characteristics of winter habitat, *etc.* (Chapter 5).

Acknowledgments

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Tables

Table 3-1. Number of tags recovered (for each species, island, year) and number of birds for which each type of data could be determined.

Species	Island	Year	Tags recovered	Departure date	End-of-breeding and departure dates	Pairs with simultaneous data
Whiskered Auklets	Buldir	2013	12	n/a	n/a	n/a
		2014	5	n/a	n/a	n/a
	Total		**17**	**n/a**	**n/a**	**n/a**
Parakeet Auklets	Buldir	2013	11	11	10	1
		2014	35	35	16	12
	Gareloi	2013	3	3	0	1
		2014	15	15	0	6
	Total		**64**	**64**	**26**	**20**
Crested Auklets	Buldir	2013	25	21	18	0
		2014	31	26	16	0
	Gareloi	2013	21	11	11	0
		2014	21	15	3	3
	Total		**98**	**73**	**48**	**3**

Figures

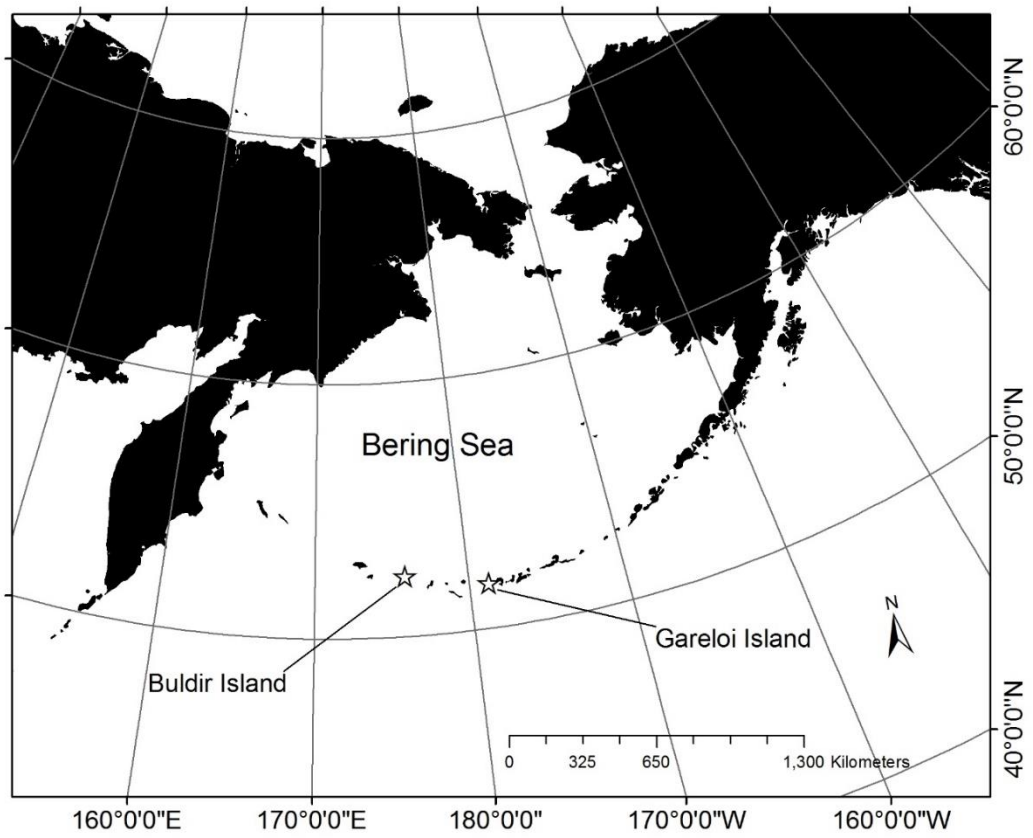

Figure 3-1. Location of colonies used in this tracking study (stars). Breeding adults were tagged on Buldir (Crested, Parakeet and Whiskered auklets) and Gareloi (Crested and Parakeet auklets) Islands in 2013 and 2014.

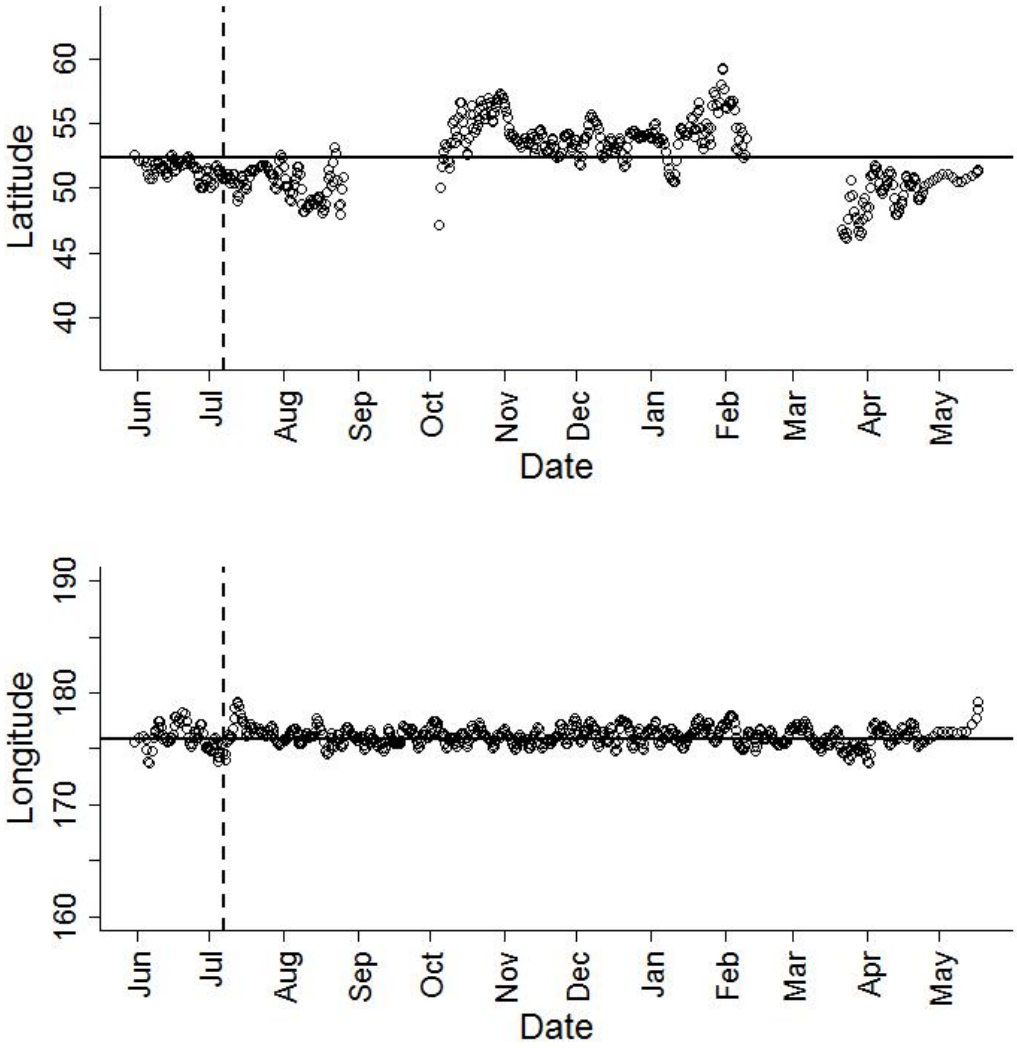

Figure 3-2. Example plot of latitude and longitude (on a 360^{o} scale) over time for one Whiskered Auklet (E828). Horizontal lines show the colony location. Dashed vertical lines show breeding cessation date. I was unable to assign departure dates for this species because they remain at/near the colony year-round. Note increased error in latitude around the edges of the equinox gaps.

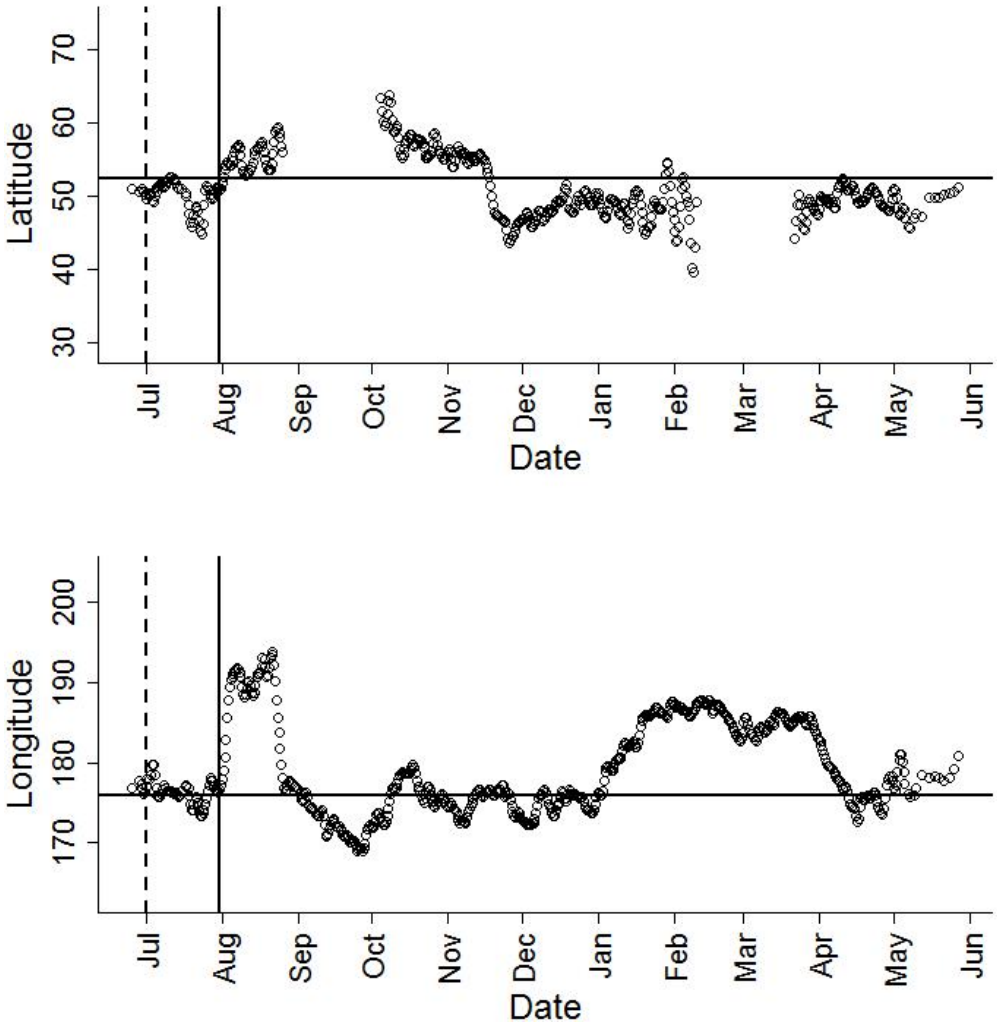

Figure 3-3. Example plot of latitude and longitude (on a 360^{o} scale) over time for one Parakeet Auklet (L469). Horizontal lines represent the colony location. Dashed vertical lines show breeding cessation date, and solid vertical lines the estimated departure date. Lag for this individual: 30 days.

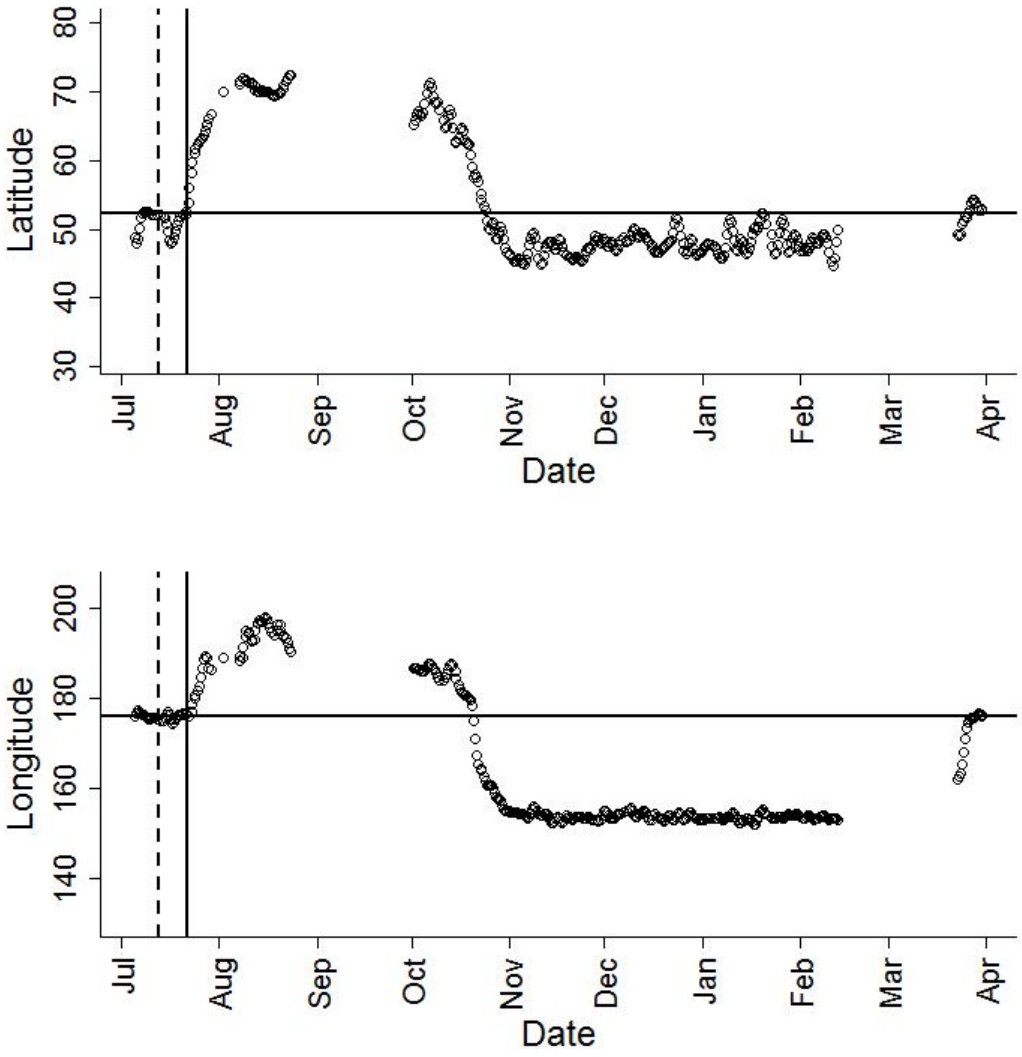

Figure 3-4. Example plot of latitude and longitude (on a 360^{o} scale) over time for one Crested Auklet (L812). Horizontal lines represent the colony location. Dashed vertical lines show breeding cessation date, and solid vertical lines the estimated departure date. Lag for this individual: 9 days.

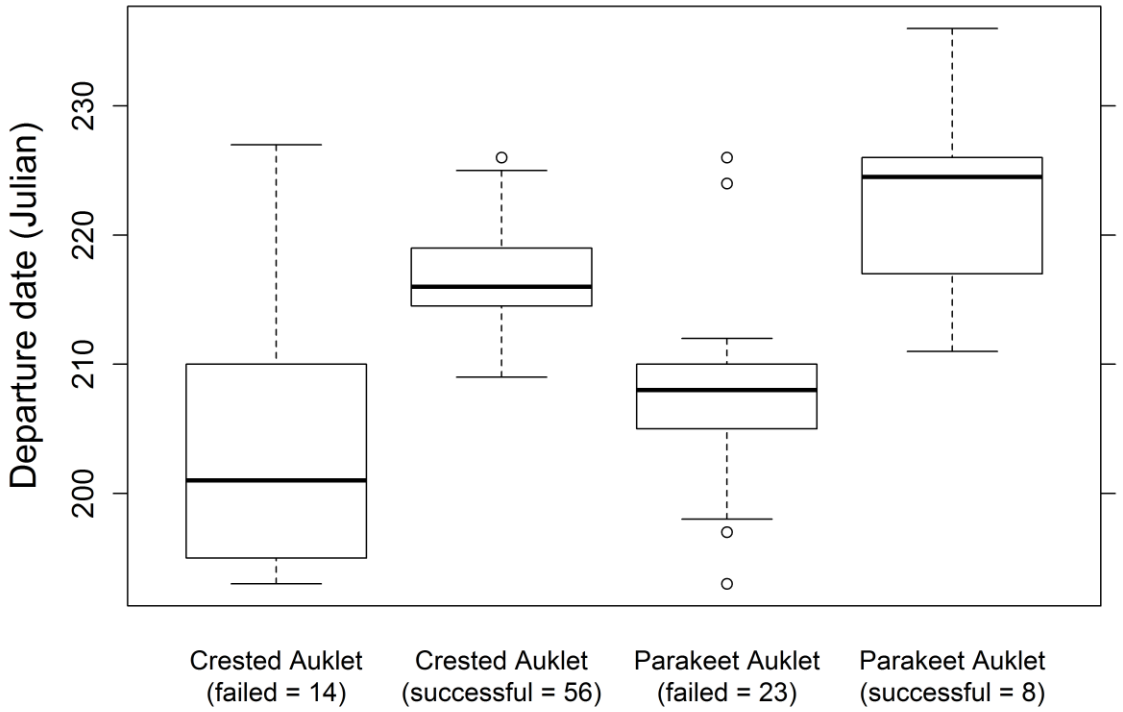

Figure 3-5. Departure date (Julian) varies depending on species and nest fate. Note: nests with unknown fate were excluded from statistical analysis of fate.

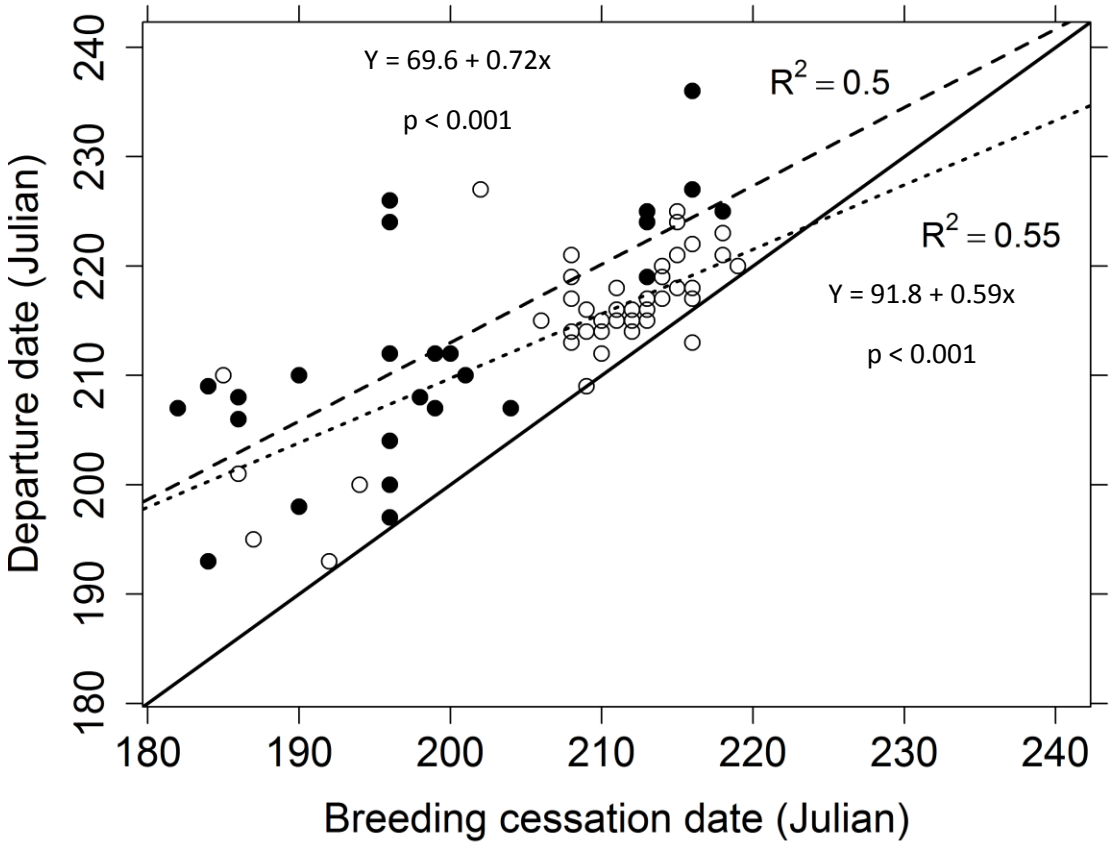

Figure 3-6. Significant positive relationship between breeding cessation date and departure date is tighter for later end dates (mostly successful breeders) than earlier end dates (mostly failed breeders). Points above the 1:1 line (solid line) depict a lag between breeding cessation and departure from the colony. Parakeet Auklets (solid circles; dashed regression line), Crested Auklets (hollow circles; dotted regression line).

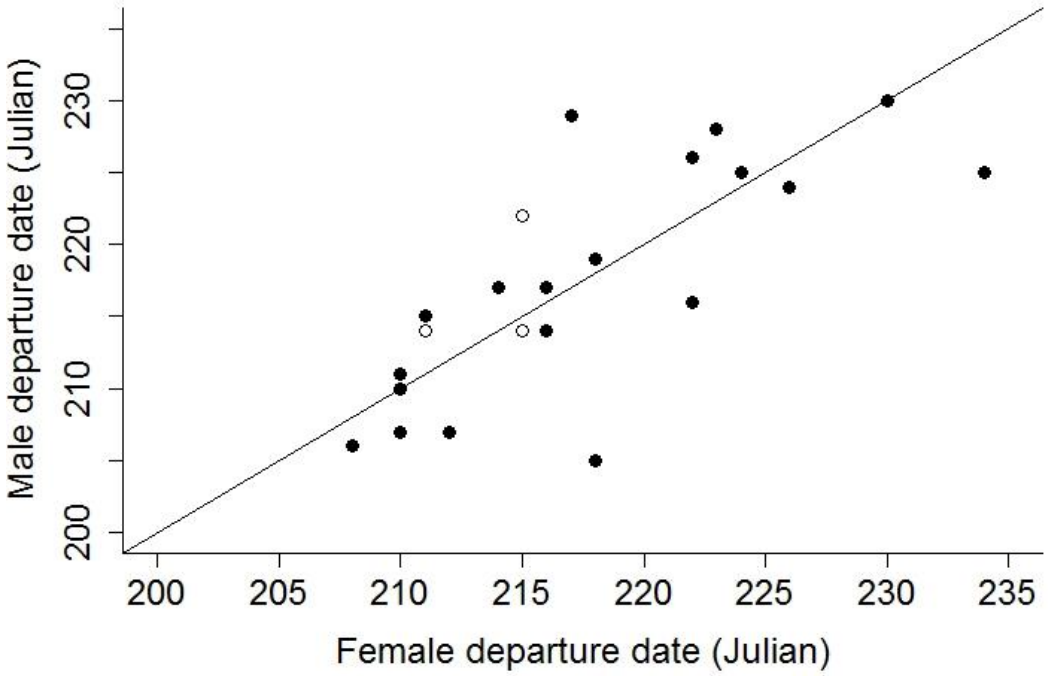

Figure 3-7. Both members of breeding pairs leave at a similar date. 1:1 line shows identical departure dates for both members of the pair. Parakeet Auklets (filled circles), Crested Auklets (hollow circles).

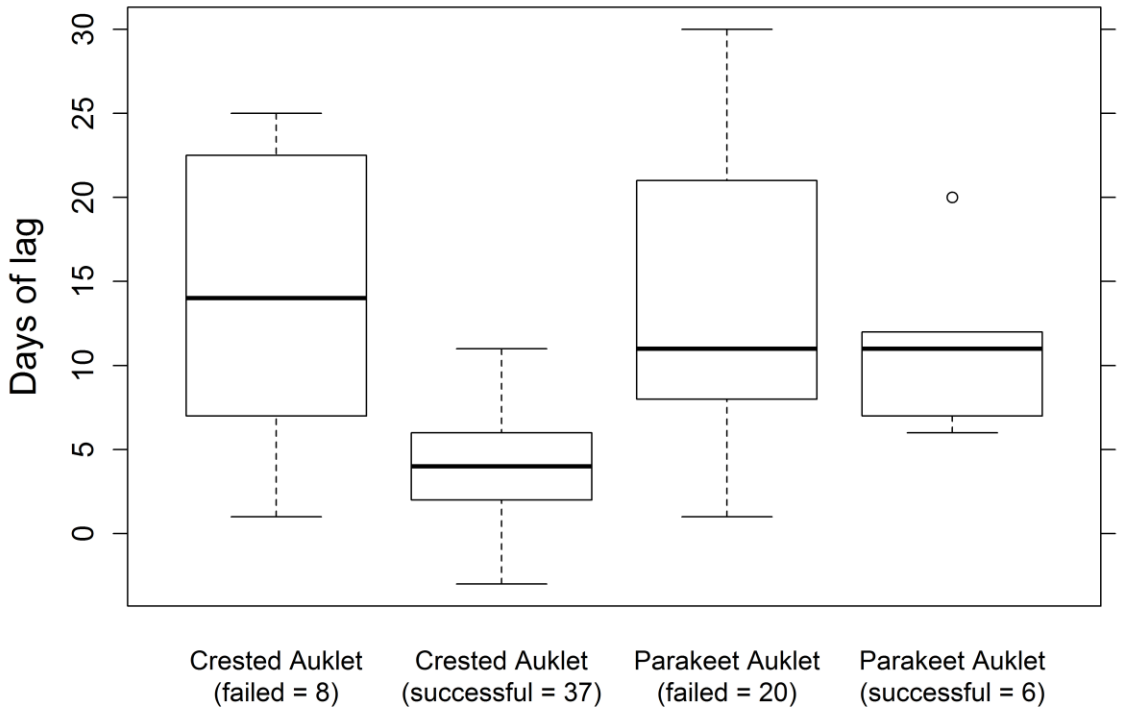

Figure 3-8. Number of days of lag between breeding cessation and departure from the vicinity of the colony depends on species and nest fate.

CHAPTER 4: YEAR-ROUND RESIDENCE AT THE COLONY CONFIRMED IN A SUBARCTIC SEABIRD

Abstract

Seabirds with limited flight capacity must forage near their breeding sites when incubating and provisioning offspring, but during the non-breeding season are free to migrate to more favorable foraging habitat. The Whiskered Auklet (*Aethia pygmaea*) is a rare example of a non-migratory seabird. At-sea surveys show that Whiskered Auklet distribution is largely restricted to areas near the Aleutian Islands. However, winter survey coverage is limited and provides no information about the colony-of-origin of sighted birds. There are also anecdotal reports of individuals on land periodically during the winter, but direct evidence that Whiskered Auklets are resident at their colonies year-round is lacking. To address this, I used geolocation tracking tags deployed on Whiskered Auklets breeding at Buldir Island, Aleutian Islands, Alaska, and Song Meters programmed to record periodically throughout the non-breeding season during times of peak Whiskered Auklet activity. Whiskered Auklets (n=17) breeding at Buldir were distributed near the island all year (average distance 212 km; within the range of error), and audio recordings confirmed their presence at least from March to October. Immersion sensors showed that they roosted on land at night year-round, except for trips to sea during full moons. My data show that Whiskered Auklets from this colony are non-migratory. However, these findings may not apply to colonies in the Sea of Okhotsk, which are surrounded by pack ice in winter, and so those populations are likely migratory to some degree. Winter residence at most colonies (leading to reduced mixing among populations) would be consistent with clinal variation observed in the Whiskered Auklet,

and the stronger genetic differentiation among Whiskered Auklet colonies compared to the congeneric Crested Auklet.

Introduction

The Whiskered Auklet is a small (mean mass 112 g) planktivorous alcid endemic to the Aleutian, Commander, and Kuril Islands (Byrd & Williams 1993, Zubakin & Konyukhov 2001). It is a species of conservation concern, and is considered vulnerable to oil spills, invasive mammalian predators, and other threats due to its restricted distribution and its year-round presence in Aleutian passes (Troy & Bradstreet 1991, Troy 1991, Williams *et al.* 2003, NPRB 2005). Juvenile Whiskered Auklets (unlike other auklet species) are known to return to sleep on land at the colony in the weeks and months after fledging (Stejneger 1885, Byrd & Gibson 1980, Zubakin & Konyukhov 2001), and there are anecdotal reports of adults on land in winter (Stejneger 1885, Murie 1936, 1959, Dick & Donaldson 1978, Zubakin & Konyukhov 2001). Due to a lack of year-round tracking data, the degree to which Whiskered Auklet populations are or are not migratory remains unconfirmed. Migration to and from a small proportion of breeding sites (*i.e.*, Iony Island, 56º24’ N, 143º22’ E; Penzhin Bay, 62º20’ N, 163º28’ E) would appear to be inevitable because they, unlike the Aleutians, lie within the mean annual limit of continuous ice cover in the Sea of Okhotsk (Gaston and Jones 1998).

Data from ship-based surveys show that Whiskered Auklet winter distribution at sea is largely restricted to areas within a few kilometres of the Aleutian Islands (Byrd & Williams 1993, NPPSD 2015). However, winter survey coverage is limited (NPPSD 2015), and provides no information as to the colony-of-origin of sighted birds. Analyses

of long-term monitoring data have shown that Whiskered Auklet productivity and survival on Buldir Island depend mainly on local conditions the previous winter and spring (Jones *et al.* 2007, Bond *et al.* 2011a), which is consistent with Whiskered Auklets wintering near their breeding sites. It is also possible that Whiskered Auklets, although remaining in the Aleutians, disperse along the island chain to concentrate at certain hotspots like Unimak Pass in the Eastern Aleutians (Troy & Bradstreet 1991). This alternative hypothesis is somewhat supported by surveys showing a more clumped at-sea distribution of Whiskered Auklets in spring, followed by a dispersal into smaller flocks spread over a broader area during the breeding season (Byrd & Gibson 1980).

The development of small, light-weight geolocation devices (Wilson & Vandenabeele 2012) has only recently allowed the tagging of birds of this size, enabling us to track the winter movements of individuals from a known colony. My objectives for this study were to discover whether Whiskered Auklets are year-round residents near their breeding site at Buldir Island, Alaska, and to describe their over-wintering behavior using tracking tags with immersion sensors and automated digital audio recordings taken at the colony site.

Methods

Study area

This study was conducted at Buldir Island, Aleutian Islands, Alaska (part of the Alaska Maritime National Wildlife Refuge), located at the approximate geographic center of this species' world range (Gaston and Jones 1998). Breeding sites (crevices and burrows) used were concentrated at Main Talus (52°22'N, 175°54'E) and Northwest Ridge

(52º22'N, 175º52'E), with additional sites located along the rocky cliffs of the northern shore (see site descriptions in Knudtson and Byrd 1982, Hipfner and Byrd 1993, Jones *et al.* 2007). These sites were spread across a variety of habitats (*e.g.*, rocky talus slopes, vegetated hillsides) representative of most Whiskered Auklets breeding at Buldir.

Device attachment

I attached 1g light-based archival geolocation tags (hereafter 'tags'; Intigeo C65, 14 x 8 x 6 mm, Migrate Technology; total attachment 2g, 1.8% body mass) to 23 Whiskered Auklets in 2013 (14 female, 9 male), and 25 in 2014 (10 female, 15 male). Birds were removed from crevices by hand, or using a long, blunt metal hook placed around the tarsus/tibia. I gave each adult a numbered aluminum band, and a custom-made Darvic color-band with a flattened side to which tags were attached with a two part marine epoxy and further secured with a cable tie. I compared tagged birds to controls to assess potential negative effects of tags on reproduction and return rates (Chapter 2). I also pulled breast feathers for genetic sex determination (Fridolfsson and Ellegren 1999) at the Genomics and Proteomics Facility at Memorial University of Newfoundland.

Tracking data processing

I deployed 5 tags for 13 days in June 2014 on a hilltop near the colony as an open-sky calibration to determine an appropriate elevation angle for this region to use as a parameter when estimating location from the sunrise/sunset data recorded by the tags (Lisovski *et al.* 2012). The resulting elevation angle (-5.6, threshold = 2) was evaluated for each bird using breeding season data (birds known to be at/near the colony), and was found to be acceptable in most cases. For a few individuals this angle resulted in a

distribution of points that did not overlap with the island (skewed too far south), and in these cases I shifted the angle until the breeding season data overlapped with the known location of the birds. I used IntiProc v1.03 (Migrate Technology Ltd) software (based on the GeoLight 2.0 R package; Lisovski & Hahn 2012) to process the raw light curves provided by the geolocation tags. I scored each sunrise/sunset event based on the amount of shading apparent in the light curve, which corresponds with error in location estimates (Lisovski and Hahn 2012). I then mapped the individual points. Obvious outliers that were also associated with a low score due to tag shading were removed, as were points during the equinoxes (9 Sept – 18 Oct, 24 Feb – 4 Apr) when day lengths around the planet are too similar for reliable estimates of latitude (Hill and Braun 2001). I smoothed the data twice (Phillips *et al.* 2004), using a 3-day running average, with fixed origin points at the beginning and end of each track and of equinox exclusion periods (Hedd *et al.* 2012). To map the resulting location points, I created a kernel density surface with Geospatial Modelling Environment (Beyer 2015), using the plug-in method for bandwidth selection (Sheather and Jones 1991, Jones et al 1996) and a cell size of 1 km. For display purposes, I then calculated percent volume contours representing 25, 50, and 80 % of locations. As a control to evaluate the accuracy of the tags, I deployed 5 tags at a fixed location on a pole near the colony for ~11 months. Data from these tags were then processed in the same way as the bird-borne tags.

Immersion data

Tags were programmed to record every 30 seconds whether or not the tag was wet (immersed in salt water) using a conductivity sensor (Fox 2015). I processed the data

from each individual in R v3.1.1 (R Core Team 2014; code adapted from Hedd *et al.* 2012) to calculate the percent of time the tag was dry during each day or night period (based on the sunrise/sunset times recorded by the tags). I then averaged these values across all birds for each period to create a plot illustrating habitat use over time.

Audio recordings

To confirm that Whiskered Auklets remained at the colony year-round, I deployed two Song Meter SM2 recording units (Wildlife Acoustics, Inc.) in areas of high Whiskered Auklet breeding site density at the Main Talus colony from 29 July 2014 – 1 April 2015. Song Meters were programmed to record every five days throughout the non-breeding season, and recordings were made in six five-minute bouts during times of peak Whiskered Auklet surface activity (three at 30-minute intervals leading up to sunrise, and three at one-hour intervals after sunset; Bradstreet & Herter 1991). I scored each five-minute recording on a scale of 0-6 based on the amount of background noise (from wind and waves), and calculated an average noise score for each day (averaged across the six recordings). Recordings ranged from being almost completely free of noise (score of 0) to being unusable due to static from high winds (score of 6). I listened to recordings, and confirmed the presence of Whiskered Auklet vocalizations by reviewing spectrograms using Song Scope 4.1.3A (Wildlife Acoustics, Inc.). I then gave each day a presence score (0-6) based on how many of the six recordings that day contained Whiskered Auklet calls. Noise scores were plotted alongside presence scores (Fig. 4-6) and used to evaluate whether an absence of identifiable vocalizations in the recordings were likely to reflect an absence of birds, or were a by-product of poor recording quality.

Results

I recovered tags from a total of 17 Whiskered Auklets (2013-2014: 7 females and 5 males; 2014-2015: 3 females and 2 males).

Tracking data

Whiskered Auklet tracking data (Fig. 4-1A) form an elliptical distribution similar to that of stationary control tags (Fig. 4-1B), but with greater dispersion due to more variable shading of the tag caused by the birds' behaviour (Phillips *et al.* 2004). Recorded positions of five control tags were, on average, 120 km (coefficient of variation CV=0.96, n=2217) from the known location of deployment (113 km in latitude, CV=1.04, n=2217; 24 km in longitude, CV=0.77, n=2217). Whiskered Auklet positions averaged 212 km (CV=0.88, n=8049) from the colony (199 km in latitude, CV=0.95, n=8049; 49 km in longitude, CV=0.99, n=8049).

Immersion data

Immersion data showed that Whiskered Auklets were generally at sea during the day for most of the year, with increases in dry readings during the breeding season (Fig. 4-2), peaking during incubation (May/June) and tapering off during chick-rearing (June/July). The data also showed that these birds were dry at night year-round. For comparison, I present the same data from congeneric Parakeet (Fig. 4-3; Chapter 5) and Crested auklets (Fig. 4-4; K. F. Robbins unpublished data), collected and processed in the same way. These species show a pattern of behaviour more typical of seabirds, spending the majority of their time (day and night) on the water. Regularly spaced spikes in wet readings can be seen at night in the Whiskered Auklet data (Fig. 4-3). These trips to sea

at night are more evident in a plot overlaying all individual data (Fig. 4-5) than in the averages (Fig. 4-2), and most coincided with the timing of the full moons (Fig. 4-5).

Audio recordings

One of the Song Meters failed. The second produced 251 individual recordings totaling 1255 min from 29 July 2014 to 1 April 2015. The latest date at which I could confirm the presence of adult Whiskered Auklets at this part of the colony was 9 October 2014, and the earliest 8 March 2015 (Fig. 4-6). Calls were detected mostly in morning recordings July-October (10 of 11), and in night recordings March-April (5 of 7). Even during the breeding season, when Whiskered Auklets were known to be present in the area, not all recordings contained identifiable calls.

Discussion

My data support the conclusion that Whiskered Auklets breeding at Buldir are non-migratory. Tracked individuals were distributed near the island during the non-breeding season (Fig. 4-1B), and audio recordings confirmed their presence at the colony site from at least March to October (Fig. 4-6). Unlike their congeners (Figs. 4-3, 4-4), Whiskered Auklets roosted on land at night year-round (Fig. 4-2), except for occasional trips to sea during full moon periods (Fig. 4-5), presumably to forage when there was sufficient light and/or stronger tidal currents (Jones *et al.* 2002, Paredes *et al.* 2008). Common Murres and some albatrosses are known to take advantage of the increased visibility on moonlit nights to forage for vertically migrating prey, which are found closer to the surface at night (Phalan et al. 2007, Regular et al. 2010, 2011)

My tracking data were limited by the low precision of geolocators relative to other types of tracking tags (Wakefield *et al.* 2009). However, the distribution derived from tagged Whiskered Auklets was similar to that of stationary control tags (allowing for increased error due to shading on bird-borne tags). The average distance recorded of 212 km from the colony is within the range of error of 169-400 km reported for similar bird-borne tags in other studies (Phillips *et al.* 2004, Shaffer *et al.* 2005), and is consistent with little or no movement away from Buldir. Due to the nature of the astronomical calculations employed to determine location from light data, estimates of latitude are less precise than estimates of longitude (Hill & Braun 2001), resulting in the elliptical pattern observed in the distributions (Fig. 4-1). Regardless of the latitudinal error in the tracking data, the longitudinal accuracy was sufficient to reject the conclusion that Whiskered Auklets from this colony dispersed east-west along the Aleutian chain.

As with any tracking study, it is important to consider the potential effects that tag attachment could have on the behavior of interest (Vandenabeele *et al.* 2011). A comparison of tagged and control birds in this study showed minor decreases in chick growth, and lower adult return rates in one of the two years of the study (Chapter 2, Schacter & Jones 2017). The particularly harsh winter in the Bering Sea 2014-2015 may have been a factor in the lower return rates. Whiskered Auklet survival has been shown to vary with local winter conditions, with higher mortality in stormy winters (Jones *et al.* 2007). The burden of tags may have exacerbated this effect, if individuals that could normally compensate were not able to do so when already operating near their metabolic limit (Croll and McLaren 1993, Costa 2007, Humphreys *et al.* 2007). Due to these

effects, I cannot rule out the possibility that the behaviour recorded may differ from that occurring naturally in un-tagged individuals. However, since my results are consistent with what was already known or suspected about this species, I believe that my conclusions are well-supported.

I made the assumption that the long bouts of dry readings at night resulted from birds roosting on land. Given how close they remained to the island, it is unlikely that they were undertaking the kind of sustained nocturnal flight that would produce a similar pattern. Alternatively, in some species dry readings can occur when birds tuck their legs up out of the water while floating (*e.g.*, Fifield *et al.* 2009: Common and Thick-billed murres; Harris *et al.* 2010: Atlantic Puffins). Leg-tucking behaviour, although commonly observed in captive Horned Puffins and Thick-billed Murres, is rare in captive Parakeet Auklets (D. Zombeck, Curator of Birds, North Carolina Zoo, pers. comm.), and it is unlikely to be responsible for the dry readings that occurred in our closely related Whiskered Auklets, given their small size and the turbulent nature of the sea surface near Buldir Island.

I suggest that Whiskered Auklets' winter roosting behaviour may be an adaptation to reduce metabolic costs by avoiding cold water when not foraging. However, this behaviour also greatly increases their vulnerability to introduced mammalian predators, especially during the non-breeding season when few other prey species remain (Williams *et al.* 2003). It was not possible to determine whether the birds in our study were roosting on cliff ledges or within crevices in winter (as they do in summer). However, large deposits of weathered excrement within and just outside some breeding sites (I. L. Jones

and CRS pers. obs.) might have resulted from the birds taking shelter underground after dark. Daytime use of crevices would have been apparent in the light curves recorded by the tags.

Although I was unable to confirm year-round Whiskered Auklet presence at the colony site from sound recordings, this does not necessarily indicate their absence. The nature of the colony location (steep slope overlooking a rocky shore) made it difficult to find a sheltered place for Song Meter deployment, and many recordings were too noisy due to surf and wind to detect birds, even during the breeding season when large numbers were known to be present. It is also possible that Whiskered Auklets do not vocalize much, if at all, during the non-breeding season, or that they are using a different part of the island away from the main colony site during the height of winter. The immersion data do not suggest that the absence of calls in our recordings between October and March represents departure from the island, although the full-moon trips to sea seemed to peak during this period (Fig. 4-5).

I cannot generalize about the species as a whole based on data from one colony. Whiskered Auklets differ widely in behavior across their range. For example, Aleutian populations tend to be mainly nocturnal (Byrd and Williams 1993, Zubakin & Konyukhov 2001, Jones *et al.* 2002), while those breeding in the Sea of Okhotsk are diurnal (Andreev *et al.* 2012). Breeding islands in the Sea of Okhotsk are also surrounded by 100% pack ice cover in winter (Gaston and Jones 1998), possibly necessitating some form of migration in those populations. However, winter residence at most colonies (leading to a lack of mixing among populations) would be consistent with the clinal

variation in body size and ornamentation observed in the Whiskered Auklet (Byrd and Williams 1993), and the stronger genetic differentiation among Whiskered Auklet colonies compared to the congeneric Crested Auklet (Pshenichnikova *et al.* 2015, 2017).

Data about Whiskered Auklet winter diet are limited, but suggest a reliance on amphipods (Stejneger 1885), which make up only a minor part of their breeding season diet (Day and Byrd 1989, Bond *et al.* 2011b). Feeding experiments have shown that amphipods on their own do not provide sufficient nutrition to successfully raise a chick (Bedard 1969). The lack of migration that I observed, and the nocturnal roosting may be behavioural adaptations to minimize energy expenditure during the non-breeding season, and allow these birds to subsist on lower quality and/or less abundant prey available after the preferred copepods and euphausiids migrate to greater depths for the winter (Conover 1988, Kobari and Ikeda 1999). Further research is required to determine whether winter residence is the norm for other populations, as seems likely in the rest of their Aleutian range.

Acknowledgments

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Figures

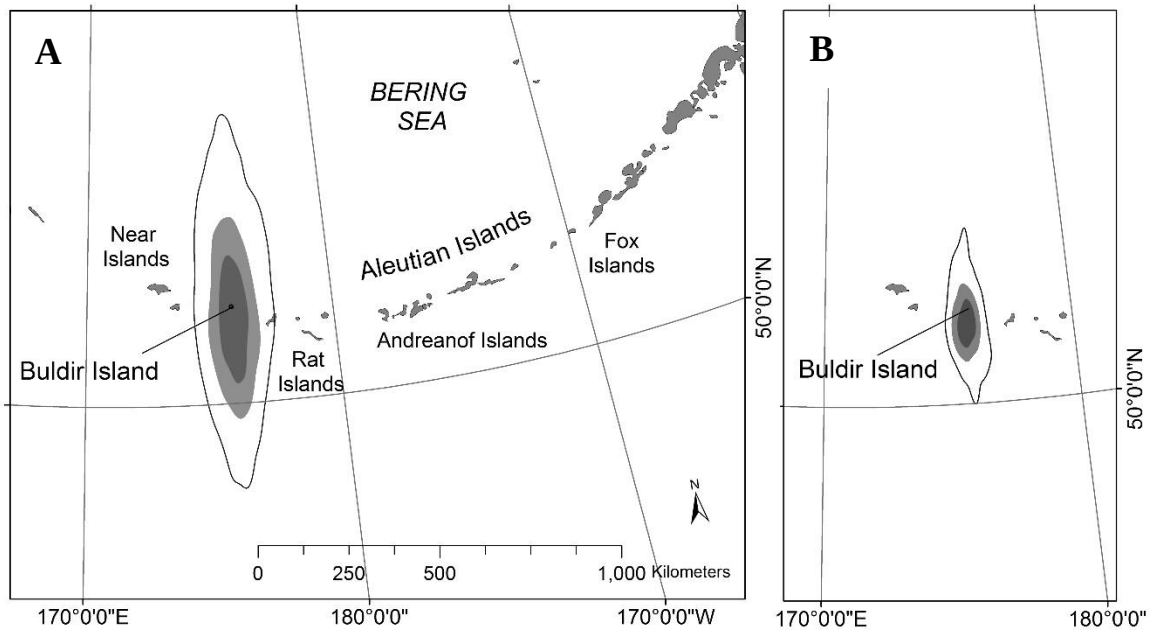

Figure 4-1. Year-round position for Intigeo C65 geolocation tags: Whiskered Auklets (A, n = 17) and stationary control tags (B, n = 5, same scale) from Buldir Island, Alaska during 2013-2015. Percent volume contours displayed for 25% (dark gray), 50% (light gray), and 80% (black outline) of points. Position error in latitude is approximately 5x larger for latitude than for longitude, due to the nature of the astronomical calculations involved in light-based geolocation.

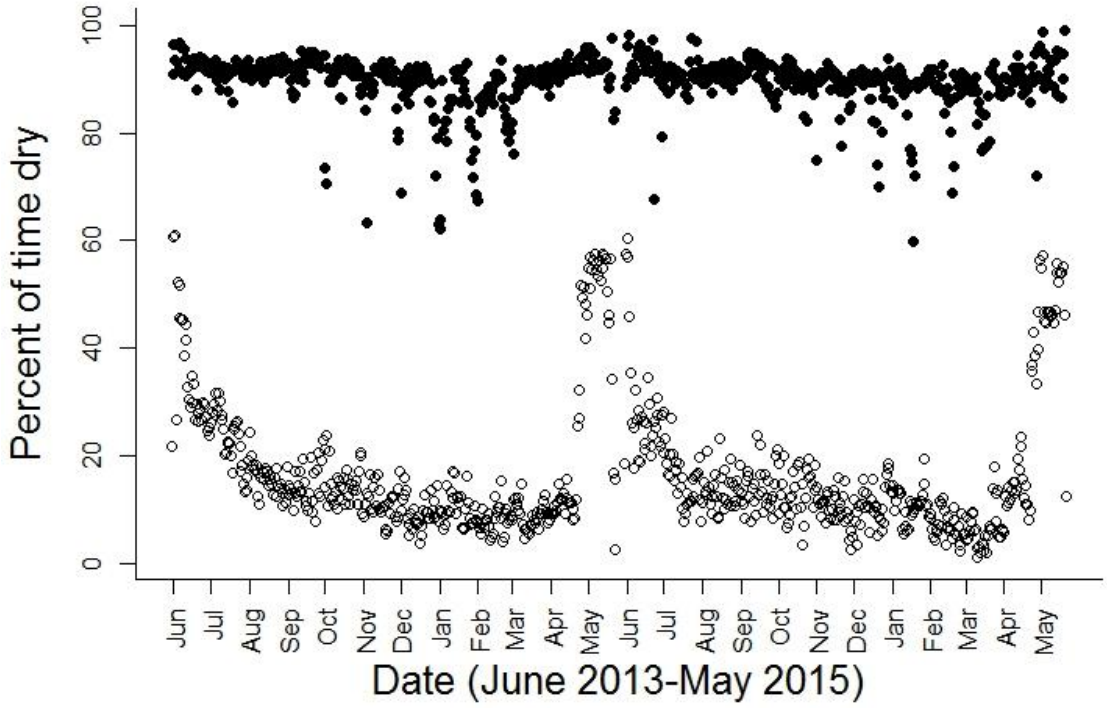

Figure 4-2. Daily percent time spent dry (not immersed in seawater) for Whiskered Auklets, separated into periods of day (hollow circles) and night (filled circles) and averaged across all individuals (2013-2014: n=12; 2014-2015: n=5).

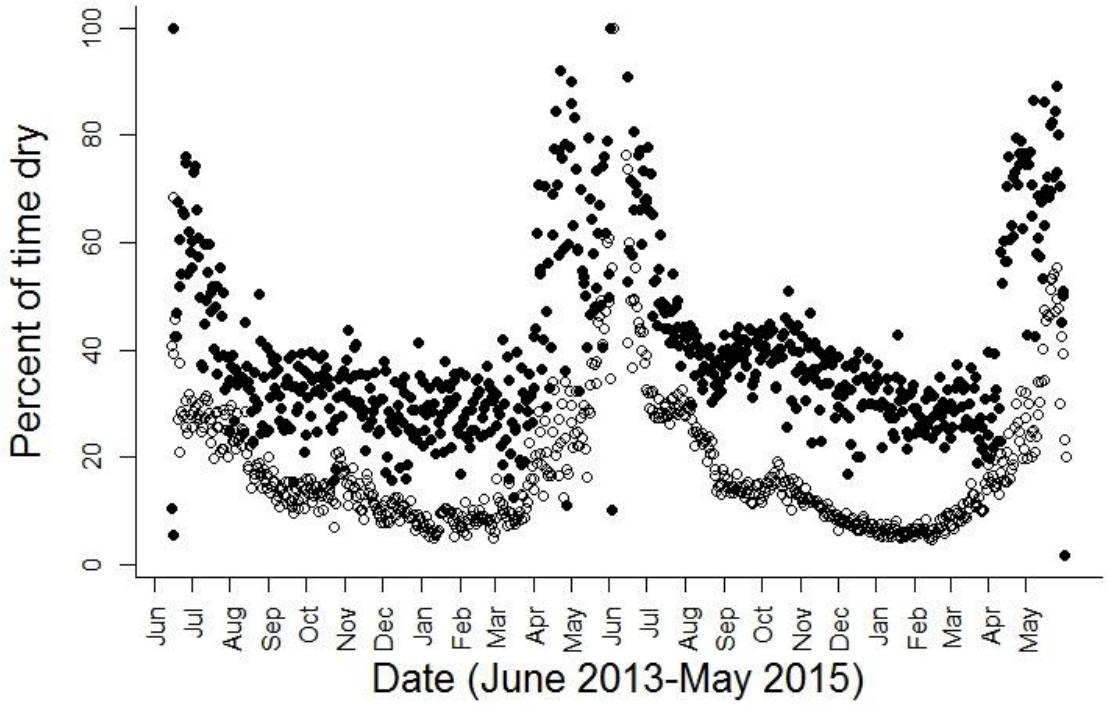

Figure 4-3. Daily percent time spent dry (not immersed in seawater) for Parakeet Auklets, separated into periods of day (hollow circles) and night (filled circles) and averaged across all individuals (2013-2014: n=14; 2014-2015: n=50).

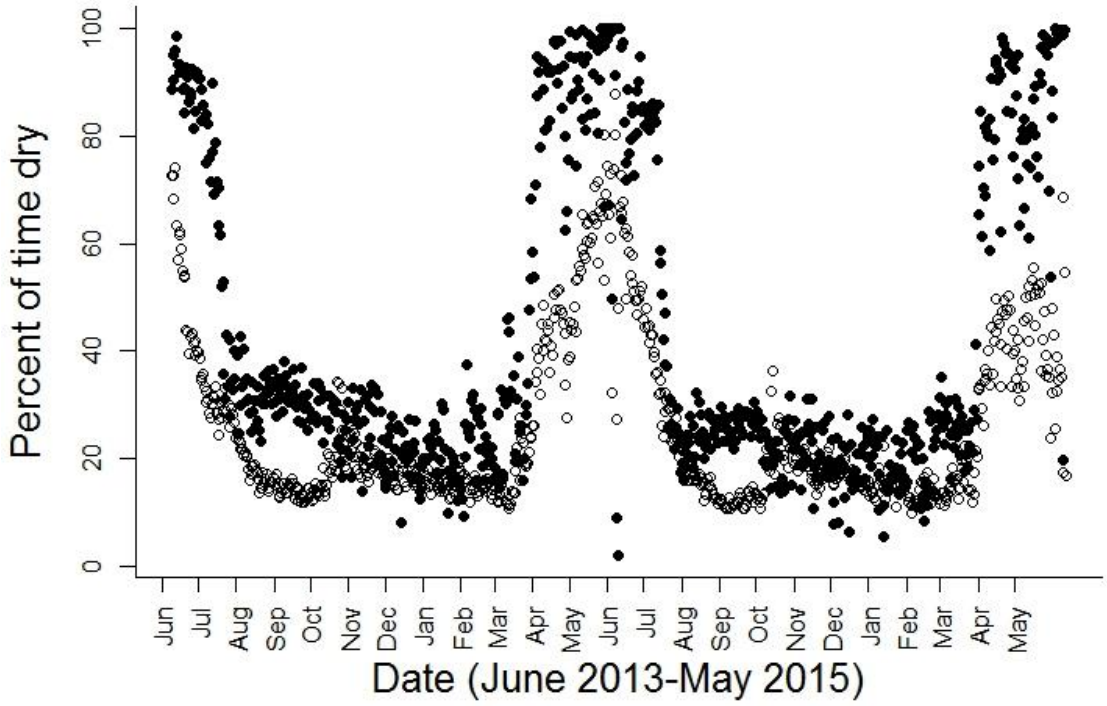

Figure 4-4. Daily percent time spent dry (not immersed in seawater) for Crested Auklets, separated into periods of day (hollow circles) and night (filled circles) and averaged across all individuals (2013-2014: n=46; 2014-2015: n=51). Data from K. F. Robbins (unpublished).

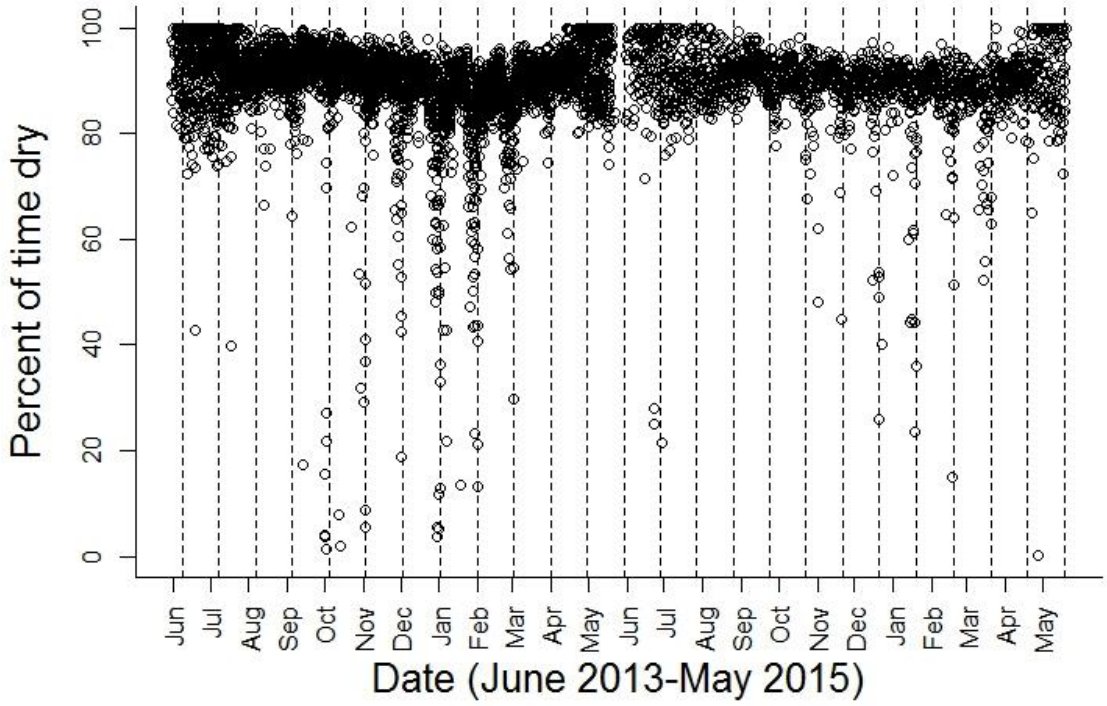

Figure 4-5. Daily percent time Whiskered Auklets spent dry (not immersed in seawater) at night, overlaying data for all individuals (2013-2014: n=12; 2014-2015: n=5). Dashed vertical lines represent timing of full moons.

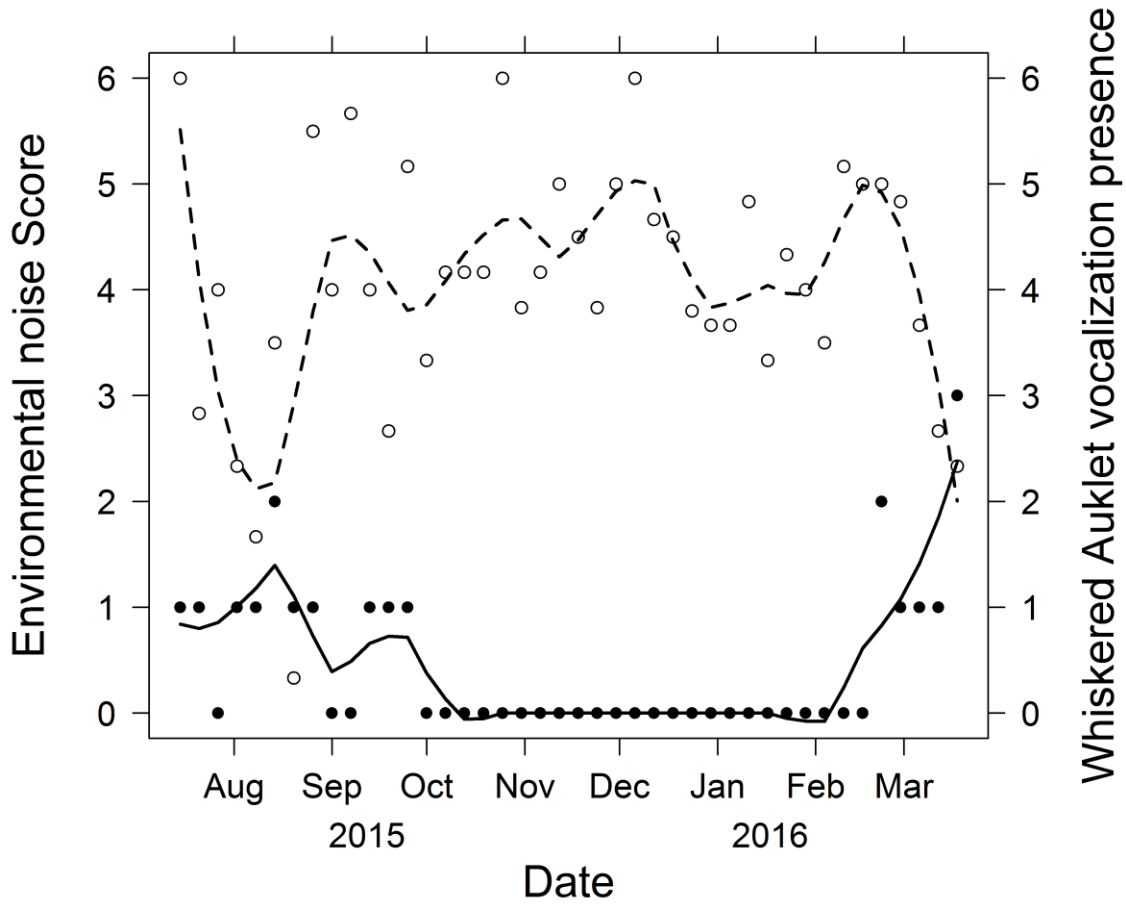

Figure 4-6. Daily scores of Whiskered Auklet vocalization presence in nighttime audio recordings from Buldir Island, Alaska during July 2014 – April 2015 (filled circles, solid line; score of 0-6 indicating how many of the recordings on that day contained at least one identifiable call), plotted alongside background surf/wind noise scores (hollow circles, dashed line; noise score 0-6 averaged across the six recordings from each day). Curves created using loess smoothing function (span = 0.25).

CHAPTER 5: THE RESIDENT-MIGRANT SPECTRUM: A TEST OF PREDICTIONS WITH *AETHIA* AUKLETS

Abstract

Seasonal movement patterns of animals range in extent from long-distance migration between distinct regions, to year-round residence, with more short-distance, dispersive migrations in between. There is also a continuum of migration type, from obligate migration (individuals must migrate), to facultative migration (extent of migration depends on local conditions) to obligate residence. Obligate migrations have a strong genetic component, and are typically long-distance, directed (LDD) migrations, characterized by consistency in timing and destination. Facultative migrations are generally short-distance and/or dispersive, more variable in timing and destination, and under less rigid genetic control. Migrations can also be classified on a quantitative continuum, based on distance travelled over time, from ballistic (highly directional, covering long distances across a barrier) to super-diffusive (directionally biased movement), to sub-diffusive (more random dispersal). I combine these aspects of migratory theory into an integrated migratory continuum from LDD migration, to intermediate migration, to residence. I then place three congeneric species of seabirds on this continuum (using *a priori* knowledge about migration timing, at-sea distribution, and behaviour) to develop and test predictions from theory. LDD migrants are expected to travel further than intermediate migrants, have greater consistency in winter habitat, and show more super-diffusive movement. I use tracking data from geolocation tags to describe for the first time the migration and wintering habitat of Parakeet Auklets (*Aethia psittacula*), and compare them with Whiskered (*A. pygmaea*) and Crested (*A. cristatella*) auklets. Existing information from ship-based surveys and breeding season monitoring

suggest placement on the migration continuum as LDD migrants (Crested Auklets), intermediate migrants (Parakeet Auklets), and residents (Whiskered Auklets). Crested Auklets are also known to make greater use of time-limited northern foraging habitat in the Chukchi Sea, therefore I expect that they will show characteristics of time-sensitive migration (as predicted by optimal migration theory), making a more rapid, direct post-breeding migration than Parakeet Auklets. Tracking data support my classification on the migratory continuum. Whiskered Auklets stayed near the colony. Crested Auklets showed greater consistency in most measures of winter habitat use, and longer migration distances than Parakeet Auklets, but did not show characteristics of time-sensitive migration as expected based on optimal migration theory. Whiskered Auklet residence is likely enabled by their less seasonal food supply, and may facilitate their longer chick-rearing period. Crested Auklets' specific diet and large flocks make them more dependent on patchy aggregations of prey, which was reflected in their consistency of habitat use, and concentration in highly productive areas. Parakeet Auklets spent most of the year in the deep Aleutian Basin (a previously unknown wintering area), where smaller flocks, and flexible diet may allow them to subsist on gelatinous zooplankton and associated amphipods. My data point to inconsistencies with some predictions of optimal migration theory (stepping-stone model with travel between discrete foraging areas). I suggest that advection-diffusion models may be more appropriate for modelling of migration in marine species crossing a more continuous environment.

Introduction

Migration has evolved in many taxa, usually as a strategy to survive in environments with a high degree of seasonality in resources (Terrill 1990, Boyle & Conway 2007, Dingle & Drake 2007, Shaw & Couzin 2013). Seasonal movements can take many forms, which may usefully be thought of as falling along a continuum of migratory behaviours (Dingle & Drake 2007, Cagnacci *et al.* 2011). At one end of the continuum is the traditional view of migration, with all individuals travelling from the breeding habitat to one or more distinct areas characterized by high winter productivity (*e.g.*, Dias *et al.* 2011, Hedd *et al.* 2012, Stenhouse *et al.* 2012). At the other end is year-round residence in the breeding area (*e.g.*, Ashmole 1962, Diamond 1975, McKnight *et al.* 2011). There are also intermediate strategies, such as dispersive migration, with individuals spreading out from the breeding site in many directions, or simply moving to different habitat in the general vicinity of the breeding site (*e.g.*, Harris *et al.* 2010, Hatch *et al.* 2010, Hedd *et al.* 2011). This continuum of spatial use patterns can also be extended to include other, related aspects of migratory behaviour. Migrations can be classified as obligate (individuals must migrate) or facultative (individuals 'choose' to migrate based on local conditions), with facultative migration forming an intermediate strategy between obligate migration and obligate residence (Berthold 1975, Terrill 1990, Newton 2012). Obligate migrations are typically long-distance, directed migrations, characterized by consistency in timing and destination among individuals (Newton 2012). Departure from the breeding ground is preemptive, occurring before local conditions deteriorate, while food is still plentiful enough to build sufficient fuel stores for the journey (Berthold 1975, 1990, Terrill 1990,

Newton 2012). Obligate migrations also tend to have a strong genetic component, with timing determined by an endogenous circannual rhythm, which can be adjusted based on external cues (such as photoperiod) that forecast future declines in local resources (Berthold 1975, Alerstam 1978, Terrill 1990). Facultative migrations are generally short-distance and/or dispersive, more variable in timing and destination, and are under less rigid genetic control (Berthold 1990, Newton 2012), often with pronounced differences between sexes and age-groups (Terrill 1990, Newton 2012). Departure is triggered directly by changes in local conditions (*e.g.*, food availability, temperature, weather, *etc*.; Terrill 1990, Dingle & Drake 2007, Newton 2012), with each bird responding according to its own internal threshold based on its individual condition, energetic requirements, *etc*. (Chapman *et al.* 2011, Newton 2012).

Attempts to build a quantitative framework for the study of migration have largely focused on birds, combining optimization analysis (Maynard Smith 1978, Stephens & Krebs 1986), with predictions based on flight mechanics (*e.g.*, Pennycuick 1975). Optimal migration theory (Alerstam & Hedenström 1998, Hedenström 2008, Alerstam 2011) assumes that selection is operating on the individual to minimize time spent travelling, net energy expenditure, or mortality risk (Alerstam 2006, Gudmundsson *et al.* 1991, Schmaljohann *et al.* 2009). Optimality models allow the development of testable predictions, and have led to productive research on many different aspects of migratory behaviour, including migration routes, timing of departure and arrival, and phenotypic flexibility (Alerstam 2001, 2011, Newton 2006, Shaw & Couzin 2013). Research and theory development have focused on two forms of gain (energy and time), rather than

risk. The energetics of flight, and of food intake at stopover sites during the migration journey suggest that migrants minimizing energy expenditure (energy-selected) should make frequent stops, carrying a lower mass of fuel to minimize the cost of flight (Alerstam & Lindström 1990). Migrants minimizing travel time (time-selected), on the other hand, should make longer trips and fewer stopovers, paying a higher energy cost to minimize the overall duration of the migration (Alerstam & Lindström 1990).

Kölzsch & Blasius (2008) proposed another quantitative framework, applying concepts from modified random walk theory (Codling *et al.* 2008) to avian migration patterns. A similarly Lagrangian approach (individual-based modeling) has a history of application in biological oceanography, most notably with passively drifting organisms (Lande & Lewis 1989). Kölzsch & Blasius (2008) use a biased random walk (BRW) model (Codling *et al.* 2008) to describe migratory movements along a continuum from diffusive to ballistic (directed) motion. Sub-diffusive motion is typical of longer stops between movement steps (Codling *et al.* 2008), super-diffusive motion results from correlated movement (directionally biased; Redner 1989), and ballistic motion indicates highly directional travel with little/no backtracking (Codling *et al.* 2008). The nature of this motion can be used to inform the categorization of migrations based on the type and extent of movements in annual migration tracks. Periodic ballistic or directionally biased super-diffusive movement, interspersed with relatively stationary interludes at wintering areas or stopover sites (Kölszch & Blasius 2008), is analogous to the classical view of long-distance, directed migration, while diffusive/sub-diffusive movement away from the breeding site is indicative of a shorter, more dispersive type of migration (Fig. 5-1C).

Residents would be expected to show minor diffusion away from the breeding site (foraging movements), with a daily reset to the point of origin (if returning to a fixed winter territory or roosting site; Fig. 5-1C).

We can view migratory behaviour as a series of inter-related continua, as described above. There is a simple quantitative continuum of migratory extent from residence to long-distance travel (Fig. 5-1A). There is also a qualitative continuum of migration type, from obligate to facultative (Fig 5-1B), which can be linked to the extent continuum. Long-distance migrations are more likely to be obligate (with consistent routes/destinations based on a genetic program) and shorter, more dispersive migrations are more likely to be facultative (based on local conditions; Newton 2012). We can extend the concept further by incorporating quantitative information about the type of movements used during migration. Long distance, directed migrations should be more likely to use rapid, ballistic (if crossing a barrier) or super-diffusive movement, while shorter, dispersive migrations should be more diffusive/sub-diffusive in nature (Fig. 5-1C). I propose a single migratory continuum (integrating all of these aspects of migration theory) with long-distance directed (LDD) migration at one extreme, residence at the other extreme, and intermediate migration in between (Fig. 5-1D). We can employ existing information about a species' anatomy, behaviour, and ecology (combined with information about migration and wintering areas when available) to posit their position on the migratory continuum, and then develop testable *a priori* predictions from migration theory to guide future research. Migration distance can be measured directly from tracking data and banding studies, but can be difficult to infer from Eulerian survey

data, since the point-of-origin of wintering birds often cannot be determined with certainty. The consistency of departure timing after breeding, however, should be measurable for many species using data collected at the breeding site, and is strongly indicative of migration type (obligate *vs*. facultative; Fig. 5-1B). Obligate, and long-distance migrants also tend to have a more developed syndrome of physiological/behavioural adaptations for the migration journey (Dingle 2006, Dingle & Drake 2007), which can often be identified independently of direct migration data. These adaptations may include increased foraging activity and rapid fat deposition (hyperphagia; McLandress & Raveling 1981, Wingfield *et al.* 1990, Dingle 2006), migratory restlessness (zugunruhe; Berthold 1975, Gwinner 1990), and longer, more streamlined wings (Mönkönnen 1995, Dingle 2006, Minias *et al.* 2015). Taken individually, most of these traits could have evolved for other purposes, but the more characteristics used, the more robust the classification can be, especially in a comparative study when ranking the degree of migratory behaviour among species. I am not advocating a fixed set of criteria for use in an *absolute* categorization of migratory behaviour, but rather a technique for the *relative* positioning of species on a continuum, with useful applications for future research (see Chapter 6). Once their places on the migration continuum are identified, we can use migration theory and information about breeding season behaviour to make specific, testable predictions about their migration journey and wintering habitat

The extent to which a migration strategy is favoured over residency depends largely on the degree of seasonality and predictability of the habitat (especially as regards

fluctuation of food resources; Boyle & Conway 2007). The Bering Sea (Fig. 5-2) is a highly seasonal habitat, with unpredictable ice cover in the winter, except for Aleutian passes. Winter seabird abundances are especially high in these passes, and along the shelf break, where strong currents and localized upwelling provide reliable concentrations of accessible zooplankton (Schneider et al 1987, Springer *et al.* 1996, Hunt 1997, Ladd *et al.* 2005, Suryan *et al.* 2006), even during autumn and winter when most zooplankton undertake a seasonal migration to greater depths (Conover 1988, Kobari and Ikeda 1999). A system of currents ("Bering Sea Green Belt"; Springer *et al.* 1996, Piatt & Springer 2003) also serves to transport nutrients and plankton from the productive shelf break region (Iverson *et al.* 1979, Cooney & Coyle 1982) north into the Chukchi Sea, an important foraging area for many seabird species (Gall *et al.* 2013, Kuletz *et al.* 2015) until the expanding pack ice drives them further south. In contrast, the deep basin of the southwestern Bering Sea (Aleutian Basin; Fig. 5-2) supports much lower densities of seabirds (Sydeman *et al.* 2010, NPPSD 2015). This region is nutrient rich, but highly stratified, with a warm, low-nutrient layer up to ~30m depth, and most nutrients occupying even deeper layers (peaking ~900m; Roden 1995, Whitledge & Luchin 1999). The basin also has very limited horizontal flow (Stabeno & Reed 1994, Roden 1995), all of which combine to make zooplankton difficult to access, especially during the winter (Conover 1988, Kobari and Ikeda 1999).

Aethia auklets breeding in the Aleutian Islands of Alaska provide an excellent system for the study of migration in general, and for an application of the migration continuum (Fig. 5-1) in particular. They breed at mixed colonies where their ranges

overlap, and their high breeding-site fidelity (returning to the same burrow/crevice) allows reliable recovery of archival tracking tags. Although migration routes and wintering areas remain poorly known, there are sufficient data available from ship-based surveys to allow the formation of reasonable hypotheses. Their breeding biology has also been well-studied at the colony (*e.g.*, Knudtson & Byrd 1982, Hipfner & Byrd 1993, Hunter *et al.* 2002), and previous research has shown pronounced differences in consistency of migration timing (Chapter 3). Despite their close relationship, the three species studied here differ in several important ways, making for an interesting comparison.

Whiskered Auklets breed at many small colonies throughout the Aleutians (Byrd *et al.* 2005). They remain near the islands year-round (Byrd & Williams 1993, NPPSD 2015), and I have shown that Whiskered Auklets breeding at one Aleutian colony (Buldir Island; Fig. 5-2) are non-migratory (residents), roosting on land at night throughout the non-breeding season (Chapter 4). It is likely that Whiskered Auklets in most parts of their range (with the probable exception of some colonies in the Sea of Okhotsk that are surrounded by ice in winter; Gaston & Jones 1998) share this behaviour (anecdotal evidence from: Stejneger 1885, Murie 1936, 1959, Dick & Donaldson 1978, Zubakin & Konyukhov 2001). Crested Auklets breed in large colonies (Byrd *et al.* 2005), and are gregarious, leaving (and returning to) the colony in large coordinated flocks to forage offshore (Bédard 1969, Gaston & Jones 1998). Their summer diet is specialized, dominated by euphausiids and calanoid copepods (Hunt *et al.* 1998, Guy *et al.* 2009, Bond *et al.* 2011), although the limited data available suggest that their winter diet may

be more varied (Bedard 1969, Troy & Bradstreet 1991). Compared with most alcids, their wings are relatively narrow and streamlined (Gaston & Jones 1998; Table 1), which allows for faster, more energy-efficient flight (Norberg 1989, Rayner 1990). However, along with other adaptations, narrower wings may also lead to tradeoffs in the form of reduced efficiency underwater and reduced dive depth (Thaxter *et al.* 2010, Elliot *et al.* 2013). I have previously shown a high degree of consistency in timing of Crested Auklet migration (Chapter 3), consistent with LDD migration (Newton 2012), and the limited data available about their non-breeding season behaviour support the same conclusion. Ship-based survey data (NPPSD 2015) show a tight coastal distribution during the winter, with large numbers of birds clustered in a few hotspots, while preliminary tracking data (n=3; Robinson 2015) suggest that they undergo a long-distance migration to two distinct wintering areas. Parakeet Auklets breed at much lower densities than Crested Auklets (Byrd *et al.* 2005), and are less gregarious, flying out to forage singly or in small groups (Bédard 1969, Gaston & Jones 1998). These differences likely continue into the non-breeding season: greater winter flock sizes were observed for Crested than Parakeet auklets during ship-based surveys (Crested Auklet average flock size 32 +/- 232, maximum 10500; Parakeet Auklet average 3 +/- 8, maximum 213, NPPSD 2015; Hunt *et al.* 1993, Gaston & Jones 1998). Little is known about Parakeet Auklet winter habitat. Ship-based surveys show a more widespread distribution than Crested Auklets, but survey coverage is limited (NPPSD 2015). Prior speculations based on sporadic winter sightings generally assumed that they disperse south of the Aleutian Islands after breeding, wintering offshore, with no evidence for long-distance migration (Gaston &

Jones 1998, Jones *et al.* 2001). Parakeet Auklets also have a more generalist diet than other auklets, including mollusks, gelatinous zooplankton, euphausiids, copepods, and larval fish (Bédard 1969, Day & Byrd 1989, Harrison 1990, Hunt *et al.* 1998), which should make them less dependent than Crested Auklets on areas of high productivity with predictably abundant prey, and likely contributes to their more dispersed at-sea distribution (Bédard 1969, Hunt *et al.* 1993). Although similar in size to Crested Auklets, Parakeet Auklets have a broader wing (lower aspect ratio; Table 1), and previous work has shown high individual variation in migration timing (Chapter 3), consistent with intermediate migration (Newton 2012). I therefore have three closely related species falling at different places on the migration continuum (Fig 5-1), from residence (Whiskered Auklets) to intermediate migration (Parakeet Auklets) to LDD migration (Crested Auklets).

The objectives of this study were: (1) to describe for the first time the migration and non-breeding habitat of Parakeet Auklets using data from geolocation tracking tags deployed at two Aleutian colonies (Crested and Whiskered auklet tracking data and wintering areas are described in detail elsewhere: KF Robbins unpublished data, Chapter 4); (2) to use geolocation tracking data to make a quantitative comparison of migration and winter habitat for Parakeet, Crested and Whiskered auklets; (3) to use this comparison to test predictions derived from theories of migration and validate my classification of these species on the migration continuum based on differences in their ecology/physiology/behaviour (Fig 5-1). Specifically, the wing morphology and consistency of migration timing (Chapter 3) in Crested Auklets suggest their

classification as LDD migrants at one extreme of the migration continuum, whereas Parakeet Auklets are more variable in their migration timing (Chapter 3), suggesting an intermediate place on the continuum. The limited *a priori* evidence available about migration distance and destination in these species is also consistent with this classification (Jones 1993, Jones *et al.* 2001, Robinson 2015, NPPSD 2015). Previous work has confirmed that Whiskered Auklets are non-migratory, at least at Buldir Island (Chapter 4), and since the extent of winter movements is likely smaller than tag accuracy (Chapter 4), in the current study I exclude Whiskered Auklets from analyses related to characteristics of winter habitat (see Methods), but include them in comparisons with the other two species when appropriate. If my ranking is valid, I would expect Crested Auklets (LDD migrants) to travel greater distances, with greater consistency in destination (within individuals, among colonies, and within the population as a whole), distance travelled, and habitat used than Parakeet Auklets, and be less likely to show differences between sexes (Terrill 1990, Newton 2012). Interspecific differences are also predicted based on the diffusive/ballistic continuum (Fig. 5-C). I expect Whiskered Auklets (residents) to show only limited diffusive movement away from the colony (due to daily foraging movements and/or tag error), Parakeet Auklets to make mostly diffusive/sub-diffusive movements (slow travel while foraging), and Crested Auklets to show super-diffusive movement, as a consequence of periodically strong directional movements toward seasonally predictable foraging hotspots. Due to their more specific diet and larger flock sizes, I also expect Crested Auklets to be more dependent on productive areas (*e.g.*, shelf/shelf-break region, northern regions where long days lead to

high primary productivity during the ice-free season), while Parakeet Auklets, which feed on a wider range of prey with more stable annual abundances can live in less productive areas (Bédard 1969, Hunt *et al.* 1993). If Crested Auklets are more likely to rely on productive northern regions than Parakeet Auklets (as seems likely given their prevalence in late summer/autumn surveys of the Chukchi Sea; Gall *et al.* 2013, Kuletz *et al.* 2015), it suggests a more time-sensitive migration, selected to maximize the use of this habitat during the ice-free season. This behaviour should be apparent in tracking data as longer bouts of flight with fewer stopovers during the autumn migration (Alerstam & Lindström 1990, Alerstam & Hedenström 1998), represented by greater weekly flight velocities and longer bouts of dry readings on tag sensors.

Methods

Study site

This study was conducted at Buldir (all three species; 52º11'N, 175º56'E) and Gareloi (Parakeet and Crested auklets only; 51º47'N, 178º47'W) Islands in the western Aleutian Islands, a part of the Alaska Maritime National Wildlife Refuge. Breeding sites (crevices and burrows) used on Buldir were concentrated at Main Talus (Whiskered and Crested auklets), Bottle Hill (Parakeet Auklets), and Northwest Ridge (Whiskered and Parakeet auklets), with additional sites located along the rocky cliffs of the northern shore (see descriptions in Knudtson and Byrd 1982, Hipfner and Byrd 1993, Jones *et al.* 2001). On Gareloi, I tagged Crested Auklets in semi-vegetated crevices in a lava flow on the southeast coast, and Parakeet Auklets breeding on a grassy hillside similar to the Northwest Ridge habitat on Buldir.

Device attachment

I used a 1g light-based archival geolocation tag (Intigeo C65, 14 x 8 x 6 mm, Migrate Technology) for all species (total attachment 2g, 1.8% for Whiskered Auklets, 0.8% for Parakeet and Crested auklets). See Table 5-2 for details of sample sizes. I also deployed 19 2g tags (LAT 2900, 15 x 8 x 7 mm, Lotek Wireless) equipped with pressure sensors on Parakeet Auklets from Buldir Island in 2013. Many of these tags malfunctioned and differences in the on-board data processing conducted by the tags made it difficult to compare the location data with the larger sample from 1g tags. I include data from the 2g tags for dive depth only. Tag sensors recorded pressure in decibars (dbar), which are roughly equivalent to 1m of depth (1dbar = ~1.02m; Lotek Wireless 2011). I tagged adults during the chick-rearing phase to minimize the likelihood of nest abandonment (Piatt *et al.* 1990, Ackerman *et al.* 2004) and maximize tag recoveries the following year (details of device attachment in Chapter 2, Schacter & Jones 2017). I also collected breast feathers for genetic sex determination (Fridolfsson and Ellegren 1999) at the Genomics and Proteomics Facility at Memorial University of Newfoundland.

Tracking data processing

I deployed five tags for 13 days in June 2014 on a hilltop near the colony as an open-sky calibration to determine an appropriate elevation angle for this region to use as a parameter when estimating location from the sunrise/sunset data recorded by the tags (Lisovski *et al.* 2012). The resulting elevation angle (-5.6^{o}, threshold = 2) was evaluated for each bird using breeding season data (birds known to be at/near the colony), and was found to be acceptable in most cases (see Chapter 3 for details). Using a single elevation

angle for a full year of tracking data leads to some seasonal north-south shift in calculated locations (Lisovski *et al.* 2012), but techniques using multiple angles require *a priori* knowledge of wintering locations and periods of residency, or assumptions about shading that were not appropriate for my data (Lisovski *et al.* 2012, S. Lisovski pers. comm.). I also deployed five tags at a known location on Buldir Island for an entire non-breeding season (Aug-May) as a control to evaluate the accuracy of the tags (average 120km, 113km longitude, 24km latitude; Chapter 4). Data from these tags were processed in the same way as the bird-borne tags.

I used IntiProc (Migrate Technology Ltd) software (based on algorithms from the GeoLight 2.0 R package, Lisovski & Hahn 2012; threshold method: DeLong *et al.* 1992, Hill & Braun 2001) to process the raw light curves provided by the geolocation tags. I scored each sunrise/sunset event according to the quality of the light curve based on the amount of shading evident. I then mapped the individual points. Obvious outliers that were also associated with a low score due to tag shading were removed, as were points near the equinoxes (9 Sept - 18 Oct, 24 Feb - 4 Apr for Parakeet and Whiskered auklets; 9 Sept - 14 Oct, 27 Feb - 3 Apr for Crested Auklets) when day lengths around the planet are too similar for reliable estimates of latitude (Hill & Braun 2001). I smoothed the data twice (Phillips *et al.* 2004), using a three day running average, with fixed origin points at the beginning and end of each track and at the beginning and end of equinox exclusion periods (Hedd *et al.* 2012). To determine the non-breeding period for Parakeet and Crested auklets I used the 90% volume contour (VC_{90}; see below) for each island's stationary control tags as a buffer. I defined the non-breeding season as the first day an

individual bird left the colony buffer (directed motion away from colony, not fluctuations due to tag error) until the last day outside the buffer. Some Parakeet Auklets stayed near the colony long after the known death/fledging of the chick, or made numerous returns to the colony area after the initial departure (Chapter 3), in which case I set the non-breeding season based on hatch date and the latest fledging estimates for that species (Williams *et al.* 2000), so as not to discount the importance of habitat near the colony. Whiskered Auklets did not leave the vicinity of the island (Chapter 4), so I determined a set non-breeding season for all individuals using a conservative estimate of laying and fledging dates (1 August – 15 April).

To map the resulting location points, I used an equal area projection (custom Albers Equal Area conic, centered on the study area: central meridian = 171 degrees longitude, latitude of origin = 40 degrees latitude, first standard parallel = 60 degrees latitude, second standard parallel = 40 degrees latitude). With Geospatial Modelling Environment software (GME; Beyer 2015), I used location points to create kernel density surfaces (a smoothed representation of the number of locations recorded in each unit of space) for each species overall (all non-breeding season location points; for display purposes), and for each individual bird separately by month (for analysis), using only months with at least 25 locations. I determined this minimum sample size based on a pilot study, in which I started with a full month of data (n=64) and systematically removed five random points until the kernel densities produced became unrepresentative of the original distribution (due to inflation, or loss of one or more areas of concentration). I used the plug-in method for bandwidth selection (Sheather and Jones 1991, Jones et al 1996) and a

cell size of 1km. I then used GME to create polygons representing percent VCs for 25, 50, 75 and 90 % of location points contained within each kernel density surface (VC_{25}, VC_{50}, VC_{75}, and VC_{90}, respectively).

Immersion data and migration velocity

Tags included a conductivity sensor, and were programmed to record every 30s whether or not the tag was wet (immersed in salt water; Fox 2015). I processed the data from each individual in R v3.1.1 (R Core Team 2014; code adapted from Hedd *et al.* 2012) to calculate the percent of time the tag was dry during each day or night period (based on the sunrise/sunset times recorded by the tags). I also calculated the duration of each bout of dry readings (consecutive periods of zero salt-water immersion). To evaluate the feasibility of using behavioural data from the immersion sensor to compare migration behaviour, I performed preliminary tests with the Parakeet Auklet data to determine if there was a link between the dry readings recorded by the tags and the distance travelled by the birds. I selected a random 5-day period early in the non-breeding season (after colony departure and before the fall equinox) for each bird and calculated distance travelled during that period using the haversine formula for great circle distance (Sinnott 1984). I then used linear models to test the effect on distance of the percent of time the tag was dry and the average duration of consecutive dry bouts during that same time period.

I calculated weekly travel velocities (km/week) to test whether Crested Auklets have a more time-sensitive migration than Parakeet Auklets. I set the beginning of the non-breeding season for each individual (see above) as day one, and grouped location

data into weeks relative to that date (to compensate for individual differences in migration timing). I excluded any individuals with large gaps in location data around that time, and any weeks that did not contain a full seven days of data. I then calculated weekly velocity of travel using the haversine formula as above (Sinnott 1984). To evaluate the type of migration movement exhibited by all three species, I used the same time-standardized data set to plot daily average root mean squared distances (rMSD) from the breeding site. I then calculated the slope (α) of a linear regression line on a log-log plot of the initial phase of migration (first 10 days) as an objective measure for classifying displacement ($\alpha = 0$: stationary, $\alpha < 0.5$: sub-diffusive; $\alpha = 0.5$: diffusive, $0.5 < \alpha < 1$: super-diffusive; $\alpha = 1$: ballistic; Codling *et al.* 2008, Kölzsch & Blasius 2008).

Spatial measurements and non-breeding habitat

I obtained data for monthly sea ice extent (in the form of polygon shapefiles for ArcGIS) from the National Snow and Ice Data Center (25km resolution; Fetterer *et al.* 2016). I then calculated the geodesic distance from the centroid (the center of gravity of the shape; Beyer 2015) of each monthly VC to the edge of the main northern ice pack and to the colony of origin (using the Near Table function in ArcGIS v.10.3). Due to the highly variable error of each individual geolocation position (Phillips *et al.* 2004, Shaffer *et al.* 2005), I could not accurately determine the total distance travelled by each bird by summing the distance between each recorded position. Instead, I measured the distance between successive monthly centroids (VC_{75}) to provide a conservative estimate of minimum distance travelled for comparison among species.

I classified Bering Sea habitat into bathymetric zones (Fig. 5-2): coastal/inner shelf (<50 m), central/middle shelf (50-100 m) and outer shelf (100 m to shelf break at 150 m), slope (150-2000 m) and basin (>2000 m). These zones correspond to distinct hydrographic domains differing in temperature, salinity, and the amount of vertical structure in the water column (Coachman 1986, Schneider *et al.* 1986). I produced polygons for each of these zones in ArcGIS using a bathymetry raster (1 km resolution; Sbrocco & Barber 2013), and determined the percent of each VC that was in each bathymetry zone as a measure of relative habitat use.

Aerodynamic calculations

During the course of field work on Buldir Island, I opportunistically collected carcasses found near the colony or on the beach. I took measurements (mass, wingspan) and made wing tracings. I photographed wing tracings with a ruler for scale, and uploaded images to ImageJ (v. 1.50i; Schneider *et al.* 2012) for additional measurements (wing length, surface area; following Pennycuick 1989). I then used these measurements to calculate aspect ratio (wingspan^2/wing area) and wing loading (Newtons/wing area), where Newtons were calculated as avian mass x 9.81ms^{-2}.

Analysis

I used the amount of overlap in distribution (kernel density) as a measure of consistency of habitat use (within individuals, colonies, species, *etc.*; McFarlane Tranquilla *et al.* 2015; Wakefield *et al.* 2015). Species with greater consistency of winter habitat use should have higher overlap among individuals, and if birds from different colonies show habitat segregation during the non-breeding season I should detect higher overlap among

individuals from the same colony. I determined overlap between kernels using the Utilization Distribution Overlap Index (UDOI; on a scale of 0-2; a modification of Hurlbert's $E/E_{uniform}$; Hurlbert 1978, Fieberg & Kochanny 2005), which takes into account the densities in each cell of the utilization distribution (kernel density surface), not just the percent of overlap of the distribution as a whole (Fieberg & Kochanny 2005). A UDOI of zero indicates no overlap in the distributions, one is equivalent to 100% overlap of two uniform distributions (*i.e.*, habitat use is fairly consistent across the whole range), and two represents a high degree of overlap between two non-uniform distributions (*i.e.*, habitat use concentrated in one or more parts of the overall range; Fieberg & Kochanny 2005). In a comparison of multiple methods, UDOI had the best performance when ranking distributions for similarity of space use (Fieberg & Kochanny 2005). I calculated the UDOI using code provided by the authors (Fieberg 2005). For individuals with two years of data, I tested for consistency in habitat use across years by comparing the amount of overlap between 2013 and 2014 kernels with the overlap between 20 random pairs of birds (10 pairs of Parakeet Auklets and 10 pairs of Crested Auklets, selected with replacement using a random number generator). Each random pair was matched by island, and contained one bird from 2013 and one from 2014. I ran a general linear model (GLM) with factors for species, comparison type (same bird in multiple years *vs.* random pair), and the interactive effect of species and comparison type. I used a similar method to compare the consistency in space use among species (comparing 40 randomly selected pairs of Crested Auklets, 20 pairs of Whiskered Auklets, and 30 pairs of Parakeet Auklets, matched by year and island; GLM with factor

for species), and among islands for each species (60 randomly selected pairs of Crested Auklets, and 48 pairs of Parakeet Auklets from the same or different islands, matched by year; GLM with factors for species, comparison type (same island *vs*. different island), year, and the interaction of species and comparison type).

All statistical analyses were carried out using R v3.1.1 (R Core Team 2014). I evaluated assumptions for the GLM by examining residual plots. If assumptions of homogeneity or normality were violated, I carried out randomization tests (Edgington 1964, Whitlock & Schluter 2009; 5000 permutations) to calculate p-values. For models of distance, I included factors for species, island, sex, year, and interactions of species and month, and species and sex. For models of bathymetry zone use, I included factors for island, year, sex, and three-way interaction of species, month and zone. I used the multcomp package in R (Hothorn *et al.* 2008, Bretz *et al.* 2010) to conduct Tukey post-hoc pairwise comparisons. To compare weekly travel velocities, I included factors for species and week, and the interaction between them. I set an *a priori* significance level of $P < 0.05$ for all tests, and considered effects where $0.05 < P < 0.1$ to be of marginal significance. Differences in variance were tested using F-ratios. Results are presented as mean +/- standard deviation (SD). When tests of multiple VCs produced similar results, I include a summary in the text, with detailed statistics for each VC in Appendix 5-1.

Results

I obtained 17 year-round tracks for Whiskered Auklets, 64 for Parakeet Auklets (includes two individuals with two years of data), and 98 for Crested Auklets (includes two individuals with two years of data. See Table 5-2 for breakdown of sample sizes).

Dive depth

I recovered pressure sensor data from 10 tagged Parakeet Auklets (6 female, 4 male). The tags failed to record details of each dive as planned, but I was able to recover the summary logs, providing daily maximum pressures for each bird. Seven tags contained approximately a full non-breeding season of data, one failed in February, and two failed in August. Individual maximum recorded depth ranged from 29-42 m (mean: 33 +/- 3.9 m), with individual average maximum daily dive depths ranging from 17-20 m (mean: 19 +/- 1.3 m). The maximum recorded depth of 42 m is similar to the predicted maximum dive depth of 43-50 m derived from mass-based models (Burger 1991), lending support to model-based dive depths calculated for the other species (Whiskered Auklets: 20-38 m; average mass of birds used in this study: 112 g; Crested Auklets: 43-50 m; average mass: 266 g, same as Parakeet Auklets), although this model does not account for differences in wing morphology, and to our knowledge there are no direct data on dive depths of the other species available for comparison.

Description of Parakeet Auklet migration and non-breeding habitat

Departure from the vicinity of the colony occurred between July 12 and Sept 6 (average Aug 3 +/- 10.4 days), 1-30 days after cessation of breeding (average 13.3 +/- 8.0 days; see detailed results in Chapter 3). Most tracked birds (66%) made an initial flight northeast to the shelf/shelf-break region (see Fig. 5-2 for map of important geographic/oceanographic features, and Fig. 5-3 for monthly distribution maps). Other common strategies were to move east along the Aleutian Islands (14% of tracked birds) or north to the Chukchi Sea/northern shelf region (17%). After the gap in data during the

fall equinox (9 Sept - 18 Oct), the majority (52%) of birds had moved into the Aleutian Basin, with some remaining in the Chukchi Sea (22%) and shelf (27%) regions (note: percentages may add up to more than 100% if some individuals used multiple habitats during a given time period). In November, most birds were concentrated in the basin (77%), with some remaining on the shelf (17%) or in the Chukchi Sea (11%). During this time, some individuals began moving west into the Kamchatka Basin (11%) or south into the North Pacific near the Aleutian chain (22%). In December, birds were split between the basin (52%) and the North Pacific (41%), with increased use of the area south of the islands in January (61%) and February (62%). Throughout the winter, a small number of birds made trips south along the Emperor Seamounts (Dec: 8%, Jan: 9%, Feb: 14%, Apr: 6%). These trips ranged in duration from 2 days to > 97 days, although many overlapped with the spring equinox period, so exact durations could not be determined. In April most birds were moving back towards the colony, with return dates ranging from 5 Apr – 14 May (average 21 Apr +/- 8.7 days). After the gap in data during the spring equinox (24 Feb - 4 Apr), some individuals were located far south of the Eastern Aleutians (as far as 29^{o}N latitude) and gradually made their way back north to the Aleutian Islands. These data may represent trips to the Northwest Hawaiian Islands (where dead/dying birds have been reported in the winter; Clapp 1986). However, due to the gap in latitude data during the equinox period, the extent and duration of these trips could not be determined. For the same reason, I could not determine how many birds made these trips, although 10-16 % showed a distinct southward trip that could not be attributed to tag error.

The overall distributions of birds from the two colonies were similar, but there were some differences, reflecting a slight east-west shift. Parakeet Auklets from Gareloi (the more eastern of our sites) were twice as likely (22% *vs.* 11%) to make an initial trip east along the islands. They were also generally more likely to be found in shelf/shelf break habitat, with a higher percentage of tagged Gareloi birds than Buldir birds occurring there in all time periods (ranging from 5.6% / 4.3% = 1.3x Buldir levels in February to 16.7% / 4.3% = 3.8x in January). Gareloi birds were less likely to be found in the Kamchatka Basin (monthly occurrence 0-5% *vs.* 9-15% for Buldir birds) and rarely travelled south along the Emperor Seamounts (0-6% *vs.* 2-20%).

Migration distances

There was no interactive effect of species and year on minimum distance travelled ($F_{2,162}$=1.69, p=0.19). There was a significant effect of species ($F_{2,162}$=82.1, p<0.001), with significant post-hoc pairwise differences among all species (p<0.001). Crested Auklet minimum winter movements averaged 6377 +/- 1775km (range 1257-11,354km), Parakeet Auklets averaged 4273 +/- 1013km (range 1316-6851km). These results are consistent with my prediction that Crested Auklets (LDD migrants) undertake a more long-distance migration than Parakeet Auklets (intermediate migrants). Whiskered Auklets (residents) covered the least distance (averaging 1885 +/- 837 km; range 879-4095km), and apparent movement in this case can be attributed largely to tag error; see Chapter 4).

There was a significant interactive effect of month and species on distance to the main northern ice pack at all VC levels (p<0.001), so each month of data was analyzed

separately. As expected, the centroids of Crested Auklet distributions were closer to the ice edge than Parakeet Auklets in August (1.8x - 2.9x closer; $F_{1,78}>60$, $p<0.001$; Appendix 5-1, Appendix 5-2) and October (2.6 - 3.8x closer; $F_{1,103}>119$, $p<0.001$, Appendix 5-1, Appendix 5-2) at all VC levels. After ice-encroachment pushed them out of the region, Crested Auklets moved southwest to their secondary wintering area (Figs. 5-4D, 5-5G-J; Robbins unpublished data) and Parakeet Auklets were closer to the ice pack in November (1.2x -1.4x closer; $F_{1,140}>16$, $p<0.001$; Appendix 5-1), December (1.7x - 1.8x closer; $F_{1,144}>184$, $p<0.001$; Appendix 5-1), January (1.8x closer; $F_{1,137}>109$, $p<0.001$; Appendix 5-1), and February (1.7x – 1.8x closer; $F_{1,130}>54$, $p<0.001$; Appendix 5-1). There was no difference in distance to ice between species in April ($F_{1,48}<2$, $p>0.1$; Appendix 5-1). Island of origin was not a significant factor in any of the models, but there were some differences between years, and males were closer to the ice than females at most contour levels in August (1.2x – 1.3x closer; $F_{1,78}>4$, $p<0.04$; Appendix 5-1). Variance in distance to ice was higher for Crested Auklets in November ($F_{89,63}>1.8$, $p<0.01$; Appendix 5-1), and February ($F_{78,63}>2.6$, $p<0.001$; Appendix 5-1). There was no difference in variance between species in other months, except for August, when Parakeet Auklets had marginally higher variance at VC_{90} ($F_{62,23}=2.14$, $p=0.046$) and VC_{75} ($F_{62,23}=2.10$, $p=0.051$).

I found no difference between species in the variance of the distance from the island of origin August-November ($F<1.6$, $p>0.09$; Appendix 5-1) or April ($F_{6,48}<2.1$, $p>0.1$; Appendix 5-1). Contrary to my predictions, Crested Auklets had higher variance (Fig. 5-5) than Parakeet Auklets in December ($F_{93,63}>2.1$, $p<0.01$; Appendix 5-1),

January ($F_{87,63}$>4.6, p<0.001; Appendix 5-1), and February ($F_{78,63}$>4.0, p<0.001; Appendix 5-1). Similar patterns occurred when I analyzed birds from the two islands separately.

Relative habitat use

There was a significant interactive effect of species, month, and bathymetry zone on relative habitat use (expressed as the percent of each VC overlapping with a given zone, 0% = no use of that habitat by an individual during that month, 100% = individual's entire distribution for that month contained within that zone) at all VC levels ($F_{28,4052}$>10, p<0.001; Appendix 5-1), so I analyzed each month separately. For each month there was also a significant interactive effect of species and bathymetry zone (F>14, p<0.001; Appendix 5-1), so I analyzed each zone separately. Results of each model are presented in Table 5-3. Crested Auklets consistently used the inner shelf zone (<50 m) more than Parakeet Auklets, although this habitat made up only a small percentage of habitat used by Crested Auklets in most months (Appendix 5-4), its main importance being in August (28-52%) and October (30-31%). Parakeet Auklets used outer shelf (100-150 m) and slope (150-2000 m) zones more than Crested Auklets in August only. The rest of the year, either Crested Auklets used them more or there was no statistically significant difference (Table 5-3). Parakeet Auklets used the basin zone (>2000 m) more than Crested Auklets throughout the year (Appendix 5-4), using this area almost exclusively (88-100%) December to April. As expected, there was a clear overall pattern of Crested Auklet use of productive shelf/slope regions, while Parakeet Auklets spent most of the year in deep basin habitat (Table 5-3, Appendix 5-4).

Consistency of space use

As expected, the non-migratory Whiskered Auklets (WHAU, residents) showed greater intraspecific consistency of space use than Crested Auklets (CRAU, LDD migrants), which in turn were more consistent than Parakeet Auklets (PAAU, intermediate migrants). Species had a significant effect on habitat overlap (UDOI) at every VC level ($F_{2,87}$>8, p<0.001; Appendix 5-1). Post-hoc pairwise comparisons showed that for VC_{90} (PAAU<CRAU: t_{87}=-2.93, p=0.012; WHAU>CRAU: t_{87}=5.01, p<0.001; WHAU>PAAU: t_{87}=7.21, p<0.001) and VC_{75} (PAAU<CRAU: t_{87}=-2.56, p-0.032; WHAU>CRAU: t_{87}=6.44, p<0.001; WHAU>PAAU: t_{87}=8.25, p<0.001) all three species were significantly different, with Whiskered Auklets having the highest overlap, followed by Crested Auklets, then Parakeet Auklets (Fig. 5-6). Whiskered Auklets had significantly higher overlap than the other species at VC_{50} (PAAU=CRAU: t_{87}=-1.72, p=0.2; WHAU>CRAU: t_{87}=4.39, p<0.001; WHAU>PAAU: t_{87}=5.60, p<0.001) and VC_{25} (PAAU=CRAU: t_{87}=-1.89, p=0.15; WHAU>CRAU: t_{87}=2.68, p=0.023; WHAU>PAAU: t_{87}=4.12, p<0.001), but there was no difference between Crested and Parakeet auklets (Fig. 5-6). I found no evidence of segregation among islands (comparison of random pairs from the same islands versus random pairs from different islands). As in the previous analysis, Crested Auklets had higher overlap than Parakeet Auklets overall ($F_{1,103}$>4, p<0.05; Appendix 5-1) at all but VC_{25} ($F_{1,103}$=2.3, p=0.13), but there was no interactive effect of species and island on overlap ($F_{1,103}$<0.76, p>0.39; Appendix 5-1), or effect of island alone ($F_{1,103}$<1.10, p>0.30; Appendix 5-1) for any VC level.

I obtained two years of tracking data for four individuals (two Parakeet Auklets, and two Crested Auklets, all from Buldir). I found a significant interactive effect of species and comparison type (same individual *vs*. random pair) on overlap for VC_{90} ($F_{1,20}$=7.38, p<0.01), so I analyzed the two species separately. There was significantly higher overlap for the same individual than for random pairs in Crested Auklets ($F_{1,10}$=10.27, p<0.01), but no difference in Parakeet Auklets ($F_{1,10}$=0.09, p=0.77). I found the same pattern of significance for VC_{75} and VC_{50}. Only species was significant for VC_{25} ($F_{1,20}$=7.19, p=0.014), where Crested Auklets had higher overlap, but most of the values were close to zero.

Immersion data and migration velocity

I found no significant relationship between the distance travelled by Parakeet Auklets and the percent of time the tag was dry ($F_{1,55}$=0.36, p=0.55) or the average duration of bouts of consecutive dry readings ($F_{1,55}$=1.10, p=0.30). Because I was unable to make a strong connection between immersion and migration behaviour, I did not proceed with further analysis of these data (see Chapter 4 for an interspecific comparison of overall immersion patterns).

A comparison of weekly travel velocities (Fig 5-7) between Parakeet and Crested auklets (the non-migratory Whiskered Auklets are included in the figures for comparison, but not in statistical tests) showed a significant interactive effect of species and week on velocity ($F_{37,2308}$=6.38, p<0.001; Fig. 5-7, Fig. 5-8). Since I am primarily interested in the initial post-breeding migration journey, I proceeded with a more detailed analysis of the first five weeks of data only. I found no interactive effect of species and week on velocity

in this first phase of migration ($F_{4,289}$=1.60, p=0.18). The effect of week was significant ($F_{4,289}$=14.8, p<0.001), with velocities dropping off rapidly after the first week, and continuing to decline with each subsequent week. There was no effect of species ($F_{1,289}$=2.63, p=0.11). Differences between species were either small, or opposite of our predictions (Parakeet Auklets had 1.7x - 3.4x higher velocities in the first two weeks, Fig. 5-8).

A plot of rMSD over time (Fig. 5-9) shows three different patterns of migration movement. Whiskered Auklets made little/no movement away from the colony. Both Parakeet and Crested auklets made a fairly direct initial departure, after which Parakeet Auklets remained relatively close to the breeding area, while Crested Auklets show evidence of at least one more major migration journey prior to a rapid return to the colony in Apr/May. However, I did not find evidence of ballistic movement in the fall migration of either species (Fig. 5-10). Regression lines fitted to the first 10 days of data (representing the initial linear phase of the rMSD curve) produced a slope (α) of 0.37 for Whiskered Auklets (sub-diffusive movement), 0.43 for Crested Auklets (slightly sub-diffusive), and 0.69 for Parakeet Auklets (slightly super-diffusive).

Aerodynamic calculations

I took measurements of carcasses for five Crested Auklets, four Parakeet Auklets, and one Whiskered Auklet collected on Buldir Island 2012-2014. Crested Auklets had the highest aspect ratio (characteristic of long distance migrations; Rayner 1990, Mönkönnen 1995) and wing loading (increased energy expenditure in flight; Pennycuick 1987), followed by Parakeet Auklets, then Whiskered Auklets (Table 5-1). The difference in

aspect ratio between Crested and Parakeet Auklets was small, but marginally significant despite the small sample sizes (Table 5-1; $F_{1,7}$=5.17, p=0.057). The values that I calculated were similar to those reported in the literature (Table 5-1, Spear & Ainley 1997). Wing loadings were highly variable, possibly due to the fact that measurements were taken from carcasses in a wide range of body condition instead of healthy, live birds.

Discussion

Overall, tracking data support predictions based on a ranking of these three species of *Aethia* auklets on a continuum of migratory behaviour from residence (Whiskered Auklets) to intermediate migration (Parakeet Auklets) to LDD migration (Crested Auklets). Crested Auklets travelled furthest on their migration (see also Robinson 2015, KF Robbins, unpublished data), followed by Parakeet Auklets, then Whiskered Auklets (previously shown to be distributed at/near the colony year-round; Chapter 4). Crested Auklets also showed greater individual consistency of migration timing (Chapter 3), and space use than Parakeet Auklets, both at the individual and at the species level (although individual consistency was based on a small sample, n=2 for each species, and should be interpreted with caution). Interspecific differences in space use were more apparent in overlap of overall range (VC_{75}, VC_{90}) than in core habitat use (VC_{25}, VC_{50}), suggesting that individual Crested Auklets were somewhat segregated at fine scales, while using the same general area. Differences in consistency of migration timing (Chapter 3) appear to continue throughout the non-breeding season, with stronger seasonal peaks of travel in Crested than Parakeet auklets (Fig. 5-7). I also found distinct differences in relative

habitat use between Crested and Parakeet auklets, with Crested Auklets more likely to be found in shallower shelf waters, and Parakeet Auklets making greater use of deep basin regions (Table 5-3, Appendix 5-4). The only exception to this pattern occurred in August, when Parakeet Auklets used more outer shelf and slope habitat. After leaving the colony, many Parakeet Auklets made a gradual migration, appearing to travel along the shelf break (Fig. 5-2), while Crested Auklets made a more direct trip north (KF Robbins, unpublished data; however, neither species' outward migration can be considered ballistic in nature; Fig. 5-10). Crested Auklets were more strongly associated with productive northern areas like the Chukchi Sea during the ice-free period (August-October) before moving south to their secondary wintering area, the timing of which matches well with the southward progression of the ice pack (KF Robbins, unpublished data). Some individual Parakeet Auklets made a similar northern migration, but it was not widespread among my sample of tagged birds.

Although most data matched well with my predictions, some did not. I did not find Crested Auklets to have lower variance than Parakeet Auklets in most of my distance measures. Instead they were more variable in distance to the ice-pack and distance from the colony in certain months, especially for the larger VCs (ice-pack: Aug, Nov, Feb, colony: Dec-Feb; Fig. 5-5). Distance to the ice-pack is likely not relevant after October, since Crested Auklets migrated southwest from the Chukchi Sea to their secondary wintering area in November (Fig. 5-4). In August a small proportion (5%) of Crested Auklets migrated east along the Aleutian chain (where they remained in the vicinity of Unimak Pass for most of the winter) instead of north (KF Robbins, unpublished data),

which could increase the variance in distance to the ice-pack. Similarly, high variance in Crested Auklet distance from colony (Fig. 5-5) December-February could result from this divergence in individual strategy (there were a few birds that split from the main Dec-Feb concentration off the Kamchatka Peninsula, moving west to the coast of northern Japan; KF Robbins, unpublished data). I expected Crested Auklets to have greater consistency of space use among colonies than Parakeet Auklets (less likely to be spatially segregated based on colony-of-origin), but neither species showed colony-related differences in spatial overlap, despite some indications of an east-west shift in Parakeet Auklet distribution in the descriptive data. I also expected that Parakeet Auklets, as facultative migrants, would be more likely to show differences between sexes. However, I found no effect of sex in either species, except that males (regardless of species) were distributed closer to the ice-pack than females in August. This difference could reflect an earlier departure from the colony by males, or increased nutritional needs post-breeding in males providing greater incentive to use or arrive early at productive northern habitat. The latter is more likely, given that I found no effect of sex on migration timing (Chapter 3). The sex ratio of tagged birds (captured during the early chick-rearing period) was slightly biased towards males (Crested Auklets: 58% male, Parakeet Auklets: 54%) and negative effects on chick growth in Parakeet Auklets were higher for tagged males than for tagged females (Chapter 2, Schacter & Jones 2017), suggesting that males may take on a greater share of nest defense and/or chick provisioning during this stage, increasing their energetic costs later in the season. Although I did confirm greater use of time-limited near-ice habitat in Crested Auklets (as expected based on survey data; NPPSD 2015), I

found no evidence that they were more time-sensitive in their fall migration than Parakeet Auklets (Fig. 5-8), although subsequent migrations between the first and second wintering areas and back to the colony in the spring seem to be more super-diffusive in nature (Fig. 5-10). Due to the limited spatial and temporal resolution of geolocation tracking data, I was not able to incorporate into my analysis the potential timing of migration to take advantage of favourable winds. This omission could lead to an incomplete picture of movement patterns in these species (*e.g.*, Åkesson & Hedenström 2000, González-Solís et al 2009, Fifield et al. 2014). Strong winds allow energy-efficient soaring, even in species with high wing-loading like alcids (Pennycuick 1987, Norberg 1990).

Despite similar breeding habitat and behaviour, the three congeneric species studied here used very different strategies for survival during the non-breeding season. Whiskered Auklets (from Buldir Island, and likely other southern colonies) are residents near the breeding site, and roost on land at night year-round (Chapter 4), an uncommon strategy in seabirds (Bridge 2006). Whiskered Auklets specialize on feeding in tide rips close to their colonies (Byrd & Gibson 1980, Herter 1991, Byrd & Williams 1993), which provide a reliable and accessible source of prey all year (Day & Byrd 1989, Holm & Burger 2002, Ladd *et al.* 2005). This foraging strategy both increases the patchiness and decreases the seasonality of their food source (factors that tend to favour residence; Shaw & Couzin 2013). Residence can also provide advantages in terms of an earlier start to the breeding season (O'Connor *et al.* 1984). Whiskered Auklets are the earliest crevice/burrow nesters on Buldir, laying eggs in mid-late May (Williams *et al.* 2000,

Mudge & Pietrzak 2015). However, they are often forced out of breeding crevices by the larger Crested Auklets later in the season, so they are unlikely to derive a territorial advantage from their early start. In addition to the earliest laying dates, Whiskered Auklets also have the longest chick rearing period of the *Aethia* auklets. Due to their nocturnality (in this part of their range), they only provision their chicks 1-2x per day, leading to slower chick growth than their diurnal congeners (Hunter *et al.* 2002). An early start to breeding may be necessary in order for the chicks to fledge before the end of the breeding season (late hatching chicks are often in poor condition and/or fail to fledge; CRS pers. obs.) and contribute to Whiskered Auklets' non-migratory strategy.

Crested Auklets undertook a directed loop-type migration to two distinct wintering areas before returning to the colony (KF Robbins, unpublished data). Their high degree of consistency in habitat use, and their aggregation in areas where a combination of currents and topography result in concentrations of accessible prey (a pattern also seen in ship-based survey data; Hunt *et al.* 1993, 1998, NPPSD 2015), suggest that Crested Auklet foraging behaviours are adapted to finding and exploiting spatially predictable aggregations of prey in regions such as the Chukchi Sea (initial main wintering area; KF Robbins unpublished data), and the Oyashio Current region (second main wintering area, and another hotspot used by many seabirds; *e.g.*, Suryan *et al.* 2006, Rayner *et al.* 2011). Crested Auklet distribution was primarily concentrated in coastal/shelf waters where a combination of upwelling and vertical mixing of the water column provides access to zooplankton, especially in late summer/early fall (Cooney 1981, Cooney & Coyle 1982, Smith & Vidal 1984). This reliance on patchy prey did not,

however, lead to a faster, more super-diffusive migration journey as expected. Instead I found that fall migration in Crested Auklets was sub-diffusive, while the more dispersive Parakeet Auklets had a super-diffusive fall migration. This pattern may be explained by differences in foraging strategy between the two species. Sub-diffusive movements can be indicative of longer stopovers between travel steps (Codling *et al.* 2008). Crested Auklet reliance on more widely dispersed concentrations of zooplankton could result in longer stopovers for re-fueling, causing a slower overall migration velocity like that observed (Fig. 5-8), while Parakeet Auklets may adopt more of a 'fly-and-forage' approach (Strandberg & Alerstam 2007, Dias *et al.* 2012) for their more dispersed prey (see below). If this is the case, Crested Auklets did not conform to the prediction (from optimal migration theory) that time-selected migrants should avoid long stopovers in order to maximize time spent flying (Alerstam & Lindström 1990). Alternatively, there may also be some social function to longer stopovers in this highly gregarious species. A more detailed investigation of stopover locations and durations in these species will be necessary to determine the reasons for this apparent deviation from predictions.

Like Crested Auklets, Parakeet Auklets used shelf/shelf-break habitat, but this accounted for only a small percentage of their habitat use most of the year (Appendix 5-4). The exception to this pattern was in August, right after completion of breeding. Late summer/early fall is the time of peak zooplankton abundance on the shelf (Cooney 1981), and this habitat may be important to build up condition after the high energy expenditure of the breeding season. Parakeet Auklets spent the rest of the year in deep basin waters, which are generally not areas of high seabird abundance (Sydeman *et al.* 2010, NPPSD

2015). The Aleutian basin is nutrient-rich at depth (Whitledge & Luchin 1999), but the water column is highly stratified, with a warm, low-nutrient surface layer, limited horizontal flow, and water too deep to allow the influence of bottom topography to concentrate zooplankton near the surface (Stabeno & Reed 1994, Roden 1995). Parakeet Auklets' greater relative use of this habitat is not likely due to any large difference in dive depth capabilities between the two species. A mass-based model of alcid dive depth predicts a maximum dive depth of 43-50m for Crested Auklets (Burger 1991). Although this model performed well for Parakeet Auklets (predicted maximum depth: 43-50m, measured maximum: 42m; Burger 1991), it does not take into account wing shape or other potential differences, and I have no direct dive depth data for Crested Auklets for comparison. They are, however, known to feed on benthic prey in waters 35m deep (Bédard 1969), so their maximum dive depth is likely at least 35m. Dive depth data, and more extensive measurements of aspect ratio in live specimens will be necessary to prove/disprove the expected trade-off between morphological adaptation for more efficient flight (higher aspect ratio, lower wing-loading) and dive depth capabilities (Thaxter *et al.* 2010, Elliot *et al.* 2013).

During the breeding season, Parakeet Auklets do not exhibit the kind of high energy, long-distance foraging flights and social behaviour performed by Crested Auklets (Gaston & Jones 1998, Jones *et al.* 2001). Possibly as a result of this (combined with more dietary flexibility), they are able to conduct their reproductive efforts at lower cost, with less decline in body condition over the course of the breeding season (Bédard 1969). If some of these behavioural differences persist in the non-breeding season, their lower

energy expenditure, and smaller flock sizes (NPPSD 2015) could allow Parakeet Auklets to subsist in less productive regions, while their generalist diet opens up a wider variety of potential wintering areas. Differences in habitat use and migratory behaviour between these species could then result from differences in foraging strategy that lead to the exploitation of different food sources during the winter. Summer diet of Parakeet Auklets is more varied than that of other auklets (Hunt *et al.* 1998), and includes large amounts of gelatinous zooplankton and the hyperiid amphipods that are associated with jellyfish (Harrison 1984, Schneider *et al.* 1986, Hunt *et al.* 1993, 1998, Mudge & Pietzrak 2015). To my knowledge, no data are available about Parakeet Auklet winter diet, though stable isotope analysis shows that they occupy a slightly higher trophic level than other auklets (Hobson *et al.* 1994). Jellyfish could provide reliable prey for Parakeet Auklets in the deep basin in winter (Hunt *et al.* 1993, Gaston & Jones 1998), and/or individual jellyfish could represent localized food patches for seabirds foraging for the amphipods and other zooplankton commensal on the jellyfish (Harrison 1984, Schneider *et al.* 1986). Jellyfish are abundant in the top 50 m of the Aleutian basin (Decker *et al.* 2014), especially at dusk when they migrate to the surface and can be concentrated in wind-driven convergences (Hamner & Schneider 1986). It has also been suggested that the unusual upcurved lower mandible of the Parakeet Auklet may be an adaptation for handling gelatinous prey, or for plucking off the associated amphipods (Gaston & Jones 1998).

The importance of the Aleutian Basin as a Parakeet Auklet wintering area was previously unknown. A review of existing information emphasized sightings along the coast of the western United States and hypothesized a southern migration into the North

Pacific (Jones *et al.* 2001), and ship-based survey data lack any coverage in the deep basin during winter (NPPSD 2015). I have also identified an apparent association with the Emperor Seamounts, and possible long-distance trips south to the Northwest Hawaiian Islands (although further investigation will be required to confirm, given the limited accuracy of geolocation tags). Seamounts are known to accelerate water flow and concentrate prey (Genin *et al.* 1986, Boehlert 1988, Koslow 1997), providing foraging habitat for many seabirds, including Cassin's Auklets (Vermeer *et al.* 1985, Yen *et al.* 2004). The 'Hawaii' trips in April could be an extension of this seamount use, but due to overlap with the equinox, I cannot make many conclusions about the timing/duration of these trips. Dead and dying Parakeet Auklets have been reported at Midway Island and Kure Atoll (Clapp 1986). My data suggest that these records were not accidental as previously reported (Jones *et al.* 2001), but more likely this is a routine spring foraging destination for some proportion of the population.

This study also has implications for the conservation and management of auklets. In addition to the use of tracking data to identify key wintering areas for these birds, the migratory continuum presented matches well with the degree of genetic structure in auklet species. Recent work has shown a high degree of genetic and phenotypic differentiation among Whiskered Auklet colonies (Pshenichnikova *et al.*, 2017), intermediate levels in Parakeet Auklets (O. S. Pshenichnikova, unpublished data), and very little in Crested Auklets (Pshenichnikova *et al.* 2015), suggesting that the non-migratory Whiskered Auklet with limited genetic connectivity among colonies might be

better managed as separate populations, while Crested Auklets likely form larger regional units.

It is important in any tracking study to consider the potential effects that tag attachment could have on migration behaviour (Vandenabeele *et al.* 2011). A comparison of tagged and control birds conducted alongside this study showed little effect of tags on Parakeet Auklets. Tagged Whiskered Auklets suffered minor decreases in chick growth, and lower adult return rates (Chapter 2; Schacter & Jones 2017). However, my results are consistent with what was already known or suspected about Whiskered Auklet winter behaviour, lending support to my conclusions for that species (see discussion in Chapter 4). An extensive experimental study of Crested Auklets showed large effects of 2g tags on return rates and behaviour (Robinson & Jones 2014), but none were found in a more limited assessment of the 1g tags used in this study (KF Robbins, unpublished data). The small sample (n=3) of migration tracks produced from the 2g tags (Robinson 2015) showed the same pattern as the data presented here (1g tags), therefore I believe it unlikely that migration was significantly affected in this species.

My tracking data are limited by the low precision of geolocation tags relative to other types of tracking devices (Wakefield *et al.* 2009). However, this study was designed to minimize that problem. I address fairly large-scale questions (tag accuracy when deployed on birds in this study was likely ~200km; see Chapter 4). I also used weekly, instead of daily velocities, and used monthly VCs (or the centroids of their distributions) as data points for most measurements, instead of using the twice-daily location points provided by the tags. While each individual location may have low accuracy, when

combined into a density surface we can be reasonably confident that the aggregate approximates the true spatial use of the bird (Marzluff *et al.* 2004, Millspaugh *et al.* 2006, Hooten *et al.* 2013). However, even with this technique, there is a certain amount of seasonal north-south shift in the data that is inevitable when one elevation angle is used to process a whole year of data (see Methods).

Although my samples sizes (in terms of number of individuals tracked) are substantial compared to most tracking studies, I cannot necessarily generalize about species as a whole based on data from one or two colonies. Whiskered Auklets breeding in the Sea of Okhotsk are surrounded by pack ice in winter (Gaston and Jones 1998), likely resulting in some form of migration in those populations. There is also evidence to suggest that eastern Aleutian colonies of Parakeet and Crested auklets have different wintering areas than those from the western Aleutian colonies studied here. Unimak Pass in the eastern Aleutians is host to large numbers of Crested Auklets during winter (Troy & Bradstreet 1991, Renner *et al.* 2008), despite being visited by only a small minority of our tagged birds (KF Robbins unpublished data). Parakeet Auklets are frequently observed offshore of Washington and California (Jones *et al.* 2001), suggesting that eastern populations may have a more coastal southward migration, and Russian populations likely winter near Sakhalin Island, the Kuril Islands, and northern Japan (Jones *et al.* 2001). Further investigation will be required to determine if the general interspecific patterns observed in my data will hold true across regions.

My data point to inconsistencies with some of the predictions of optimal migration theory. Optimal migration models are based on a stepping-stone construction

(Alerstam & Hedenström 1998, Åkesson & Hedenström 2007), with travel between discrete stopover sites and foraging areas, crossing 'barriers' where foraging is impossible or much reduced. While these models perform well for landbirds and shorebirds, the marine environment is very different. High-quality foraging habitat at sea is heterogeneously distributed (Southwood 1977, Weimerskirch 2007), but there are few true barriers that must be crossed without foraging as there are in terrestrial and coastal systems. In fact, many seabirds likely make at least partial use of a 'fly-and-forage' strategy (*e.g.,* Strandberg & Alerstam 2007, Dias *et al.* 2012). An advection-diffusion model (also known as drift-diffusion, Codling *et al.* 2008) may be a more appropriate approach for migration in marine habitats. Kölzsch & Blasius (2008) used a stepping stone construction for the test case of their diffusion model (the White Stork, a long-distance terrestrial migrant reliant on thermal soaring), describing discrete habitats connected by rapid flight. However, the concept could be extended to an advection-diffusion model. These biased random walk models incorporate diffusive movement through space and directional bias to/from breeding and wintering areas (Codling *et al.* 2008). Similar models (Lévy flight, a special case where step lengths have infinite variance; Codling *et al.* 2008) have already been used to investigate foraging movements in marine species (*e.g.,* Viswanathan *et al.* 1996, Sims *et al.* 2012, Regular *et al.* 2013, Reynolds *et al.* 2015).

For decades, ship-based surveys were the only method available for determining winter habitat use and at-sea behavior of seabirds. Increased development of tracking technology has changed that, and now tracking has become the go-to method for these

studies. However, both methods have pros and cons and are not necessarily interchangeable. Ship-based surveys are expensive and limited in the area/timespan they can cover, but offer high spatial accuracy, and provide a good snapshot of the species composition in an area, while also allowing simultaneous behavioural observations. Tracking accuracy is often low, and usefulness may be impacted by the logistics of how many colonies can be visited (especially in residents or species with low migratory connectivity among populations). However, tracking is cheaper and provides a full time-series of data for individuals of known provenance. Ship-based data provide a better overall picture of Whiskered Auklet winter range, but could not have shown the distinct separation among colonies (NPPSD 2015, Schacter & Robbins 2016). Ship-based data also miss an important wintering area for Parakeet Auklets, due to the lack of survey effort in the Aleutian Basin mid-winter, whereas Crested Auklet distributions were fairly well represented by surveys, since they use mainly use rich coastal areas, which have good survey coverage year-round. The use of available *a priori* data to identify a species' likely place on the migration continuum (Fig 5-1) could provide a useful framework for determining what kind of data collection (*e.g.,* small number of individuals from as many colonies as possible *vs*. large sample from one accessible colony combined with ship-based surveys, *etc*.) would be most effective in an investigation of migration routes and wintering areas.

Most tracking studies are primarily descriptive, focusing on the identification of important non-breeding habitat for the target species, often in combination with ship-based surveys or banding data (Bairlein 2003, Bauer *et al.* 2009, Hedd *et al.* 2011). This

kind of work is important, especially for seabirds, which are often well-studied at the breeding colonies, with far less known about how they spend the majority of the year. Tracking data allow us to map distributions, identify areas of potential conflict with human activities (*e.g.,* shipping traffic, light attraction, wind farms, *etc*.) and inform the design of marine protected areas (Hedd *et al.* 2011, Montevecchi *et al.* 2012, McFarlane-Tranquilla *et al.* 2013). Researchers have just begun to explore the potential of tracking data as a resource to test migration theories (*e.g.*, Fifield *et al.* 2014, Pérez *et al.* 2014, Reynolds *et al.* 2015), foraging ecology (*e.g.*, Regulare *et al.* 2013, Hinke *et al.* 2015, Wakefield *et al.* 2015), carry-over effects (*e.g.*, Fayet *et al.* 2016), *etc*. Migration behaviour, in particular, has been difficult to study directly before the advent of tracking technology, relying largely on mathematical modelling, combined with empirical data from banding studies, flight energetics (Alerstam & Hedenström 1998, Alerstam 2001, Newton 2006), and field research at known stopover sites when accessible (Lindström & Alerstam 1992, Creswell 1994), something rarely possible for seabirds. This has changed in recent years, with tracking data being used to test optimal migration predictions about the use of wind by migrating birds (*e.g.*, Åkesson & Hedenström 2000, Thorup *et al.* 2003, González-Solis *et al.* 2009, Fifield et al. 2014). Tracking data will be a useful tool going forward, allowing for more robust empirical testing of models, as well as improved estimation of model parameters. However, it is important to ensure that the scale of the questions being investigated is appropriate for the resolution of the spatial data available.

I have presented data for three congeneric seabird species with very different strategies for survival in the same environment during the non-breeding season. These

species (and other similar species groups) have great potential as a model system for comparative studies investigating other aspects of migration theory, especially at Buldir Island where all three are easily accessible. Tracking data are often collected simultaneously on multiple related species due to proximity of breeding grounds and relative ease of combining field work. These data (like tracking data in general) are increasingly being used to address theoretical questions, most commonly regarding spatial/ecological segregation during the non-breeding season (*e.g.*, Phillips *et al.* 2007, Orben *et al.* 2014, MacFarlane-Tranquilla *et al.* 2015). There is still much untapped potential in tracking data (especially in comparative systems) to provide empirical tests of predictions derived from ecological theory.

Developing testable predictions from theory, which can then be evaluated against experimental/observational data is key to successful scientific investigation. I have shown that tracking data can be used to address theory and play an important role in synthesizing concepts (*e.g.*, Fig. 5-1). Such synthesis is necessary to put conservation biology on a sound scientific basis. Theoretical and experimental biologists often operate in their own separate fields, rather than building off of each other's work (Galef 2009). Theoretical models (if formulated in such a way as to generate testable hypotheses; Godfray 1995) can stimulate new directions for experimental research, while empirical data should play an important role in model construction and refinement (Turelli *et al.* 2001, Galef 2009). Mathematical models are necessarily simplified representations of natural processes, involving many assumptions about the system, and small changes in these initial assumptions can have large impacts on the resulting predictions (Maynard

Smith 1978). By using empirical data to validate assumptions, and refine parameter estimates for ecological models (Maynard Smith 1978), we can improve model performance, and strengthen conclusions that form the basis of many conservation decisions. By doing so with data from a wide variety of species, we can also determine which assumptions/parameters are broadly applicable across taxa, and which may require taxon-specific estimates. The application of more data from tracking studies to theoretical questions can push science forward, and advance conservation goals, both through direct management applications of data, and contribution to ecological theory.

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Tables

Table 5-1. Measurements of auklet carcasses salvaged on Buldir Island 2012-2014, with aerodynamic calculations (following Pennycuick 1989) and data from Spear & Ainley (1997) for comparison. Note: I did not measure mass for partially consumed carcasses.

Species		Mass (g)	Wingspan (mm)	Wing area (m^2)	Wing loading (N/m^2)	Aspect ratio
Crested Auklet		275	497	0.0310	87	7.97
		155	485	0.0302	50	7.79
		327	506	0.0282	113	9.05
		249	491	0.0264	93	9.13
		NA	475	0.0285	NA	7.93
	Study average	252 +/- 72	491 +/- 12	0.0289 +/- 0.0018	86 +/- 26	8.37 +/- 0.66
	Spear & Ainley 1997[a]	277 +/- 11	480 +/- 29	0.0283 +/- 0.0034	97 +/- 11	8.2 +/- 0.50
Parakeet Auklet		260	520	0.0377	68	7.17
		240	500	0.0334	71	7.49
		NA	560	0.0393	NA	7.98
		NA	524	0.0364	NA	7.54
	Study average	250 +/- 14	526 +/- 25	0.0367 +/- 0.0025	69 +/- 2	7.55 +/- 0.33
	Spear & Ainley 1997[b]	282	502	0.0334	83	7.50
Whiskered Auklet		111	359	0.0191	57	6.76

[a] n=4

[b] n=1

Table 5-2. Sample sizes of Intigeo C-65 tags recovered with data (for each species, island, and year).

Species	Island	Year	Tags deployed	Tags recovered
Whiskered Auklets	Buldir	2013	23	12
		2014	25	5
	Total		**48**	**17**
Parakeet Auklets	Buldir	2013	16	11
		2014	47	35
	Gareloi	2013	4	3
		2014	22	15
	Total		**89**	**64**
Crested Auklets	Buldir	2013	40	25[a]
		2014	51	29
	Gareloi	2013	46	21
		2014	48	21
	Total		**185**	**96**[a]

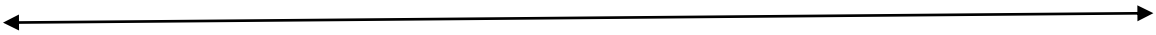
[a]Includes two tags with two years of data

Table 5-3. Summary of statistical results showing differences in relative habitat use (percent of volume contour (VC) overlapping each bathymetry zone) of Parakeet and Crested auklets over time. Significance presented after t-values (*** p<0.001, ** p<0.01, * p<0.05, Ł p<0.1), followed by a letter showing the species with greater use of that zone (C = Crested Auklet, P = Parakeet Auklet). Percent use of each zone shown in Appendix 5-3.

	Zone	90% VC	75% VC	50% VC	25% VC
Aug	<50m	t=4.3 *** C	t=5.2 *** C	t=6.1 *** C	t=6.5 *** C
n=81	50-100m	t=1.6	t=2.0 Ł C	t=1.7 Ł C	t=0.8
	100-150m	t=3.1 ** P	t=3.4 ** P	t=3.2 ** P	t=2.8 ** P
	150-2000m	t=2.8 ** P	t=3.1 ** P	t=3.5 *** P	t=3.5 *** P
	>2000m	t=3.9 *** P	t=4.5 *** P	t=4.3 *** P	t=3.7 *** P
Oct	<50m	t=6.1 *** C	t=5.5 *** C	t=4.9 *** C	t=4.4 *** C
n=106	50-100m	t=4.3 *** C	t=3.8 *** C	t=3.0 ** C	t=2.0 Ł C
	100-150m	t=2.3 * C	t=2.6 * C	t=2.5 * C	t=2.5 * C
	150-2000m	t=1.4	t=1.7	t=2.2 * C	t=2.2 * C
	>2000m	t=8.5 *** P	t=8.5 *** P	t=8.7 *** P	t=8.5 *** P
Nov	<50m	t=3.3 ** C	t=2.8 ** C	t=2.3 * C	t=2.4 * C
n=143	50-100m	t=0.7	t=0.4	t=0.2	t=0.4
	100-150m	t=0.1	t=0.1	t=0	t=0
	150-2000m	t=7.5 *** C	t=8.2 *** C	t=8.4 *** C	t=8.7 *** C
	>2000m	t=7.1 *** P	t=7.0 *** P	t=7.1 *** P	t=7.2 *** P
Dec	<50m	t=3.5 *** C	t=3.4 *** C	t=2.5 * C	t=2.2 * C
n=147	50-100m	t=0.5	t=0.4	t=0	t=0.4
	100-150m	t=1.8 Ł C	t=2.1 * C	t=1.8 Ł C	t=1.5
	150-2000m	t=14.4 *** C	t=14.4 *** C	t=13.3 *** C	t=11.5 *** C
	>2000m	t=12.8 *** P	t=13.0 *** P	t=12.4 *** P	t=10.9 *** P
Jan	<50m	t=4.2 *** C	t=3.9 *** C	t=3.1 *** C	t=2.9 ** C
n=140	50-100m	t=2.6 * C	t=2.5 * C	t=2.5 * C	t=2.5 * C
	100-150m	t=2.7 ** C	t=2.4 * C	t=1.6	t=1.0
	150-2000m	t=13.4 *** C	t=12.0 *** C	t=10.3 *** C	t=8.7 *** C
	>2000m	t=16.4 *** P	t=14.6 *** P	t=12.5 *** P	t=10.6 *** P
Feb	<50m	t=5.2 *** C	t=4.6 *** C	t=3.8 *** C	t=3.3 ** C
n=133	50-100m	t=5.7 *** C	t=5.4 *** C	t=4.2 *** C	t=3.0 ** C
	100-150m	t=6.3 *** C	t=5.6 *** C	t=4.6 *** C	t=3.3 ** C
	150-2000m	t=12.8 *** C	t=12.8 *** C	t=11.8 *** C	t=9.9 *** C
	>2000m	t=18.8 *** P	t=17.9 *** P	t=15.5 *** P	t=12.8 *** P
Apr	<50m	t=3.0 ** C	t=3.7 *** C	t=3.2 ** C	t=2.6 * C
n=51	50-100m	t=3.6 *** C	t=3.6 *** C	t=3.4 ** C	t=2.9 ** C
	100-150m	t=3.5 *** C	t=3.7 *** C	t=4.1 *** C	t=3.5 *** C
	150-2000m	t=2.3 * C	t=2.9 ** C	t=3.9 *** C	t=3.9 *** C
	>2000m	t=3.3 ** P	t=3.7 *** P	t=4.3 *** P	t=4.2 *** P

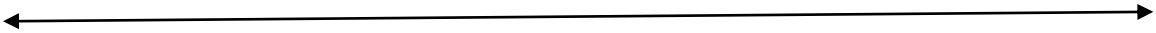
Figures

A) Extent continuum



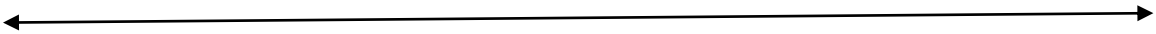
Year-round residence	*Short-medium distance migration*	*Long-distance migration*

B) Obligate/facultative continuum



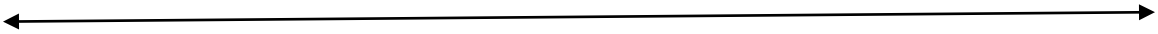
Obligate residence	*Facultative and/or partial migration*	*Obligate migration*
No easily defined departure from the breeding habitat	Often dispersive migration with variability of timing & destination	Usually long-distance directed (LDD) migration with consistency of timing & destination
Little/no adaptation for migration	Less developed syndrome of migratory adaptations	More developed syndrome of migratory adaptations

C) Diffusive/ballistic continuum



Residence	*Sub-diffusive movement*	*Super-diffusive movement*	*Ballistic movement*
Minor diffusive movement, may have daily reset to breeding site	Diffusive movement away from breeding site	Diffusive movement away from breeding site	Periods of rapid, highly directional movement
Predictable movements at local scale	Typical of motion with longer stops between movement steps	Typical of correlated (directionally biased) movements	Non-stop migration across barrier with little/no feeding habitat

D) Integrated migratory continuum, with *Aethia* species placement



Residence (Whiskered Auklet)	**Intermediate migration** (Parakeet Auklet)	**LDD migration** (Crested Auklet)

Figure 5-1. My proposed continuum of migratory behaviours, building from a quantitative spectrum (extent continuum) based on distance of migration (A), then incorporating qualitative characteristics from comparative treatment of migration (obligate/facultative continuum) (B), and quantifiable measurements based on diffusive-ballistic motion (Codling *et al.* 2008, Kölzsch & Blasius 2008) (C). I have integrated these related characteristics into an overall migratory continuum (D) and used available data to place each of my study species on that continuum.

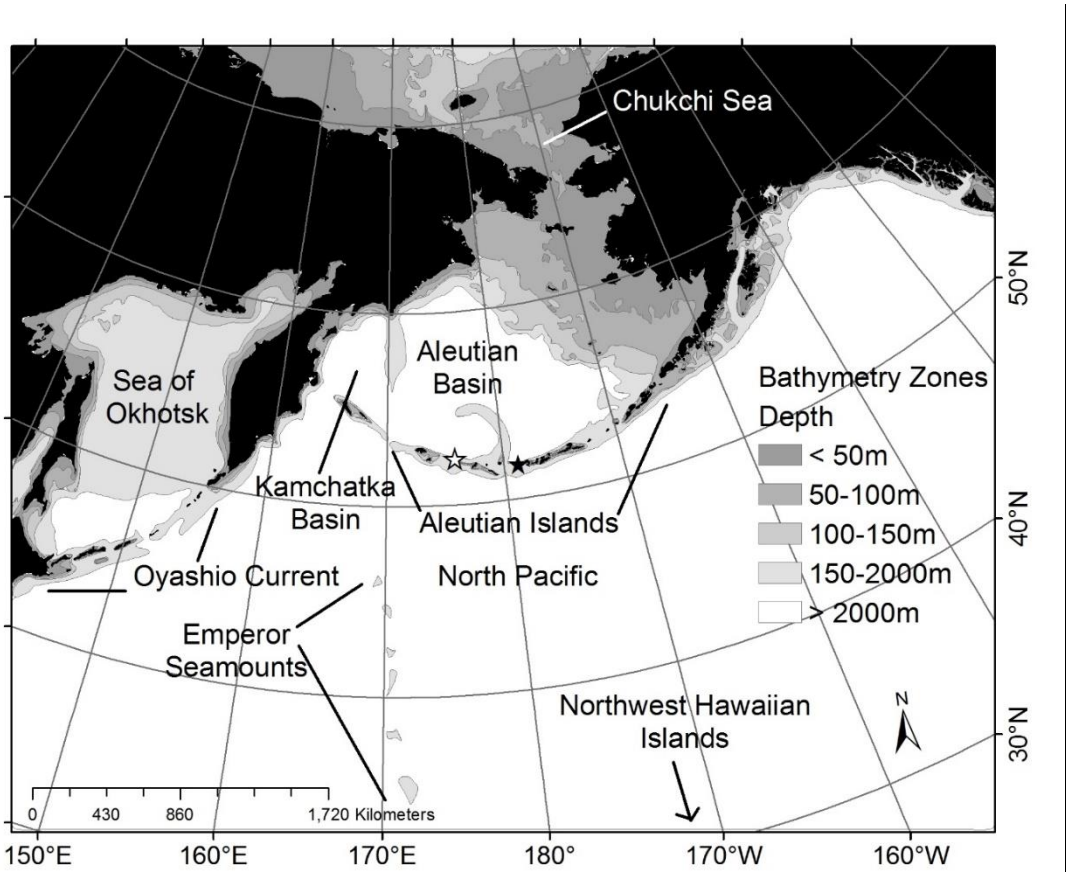


Figure 5-2. Map of the study area showing bathymetry zones used in habitat analysis and important geographic features mentioned in the text. Colony locations marked with stars (Buldir: hollow star, Gareloi: filled star). Map created in ArcGIS v.10.3 using a custom Albers equal area projection centered on the study area.

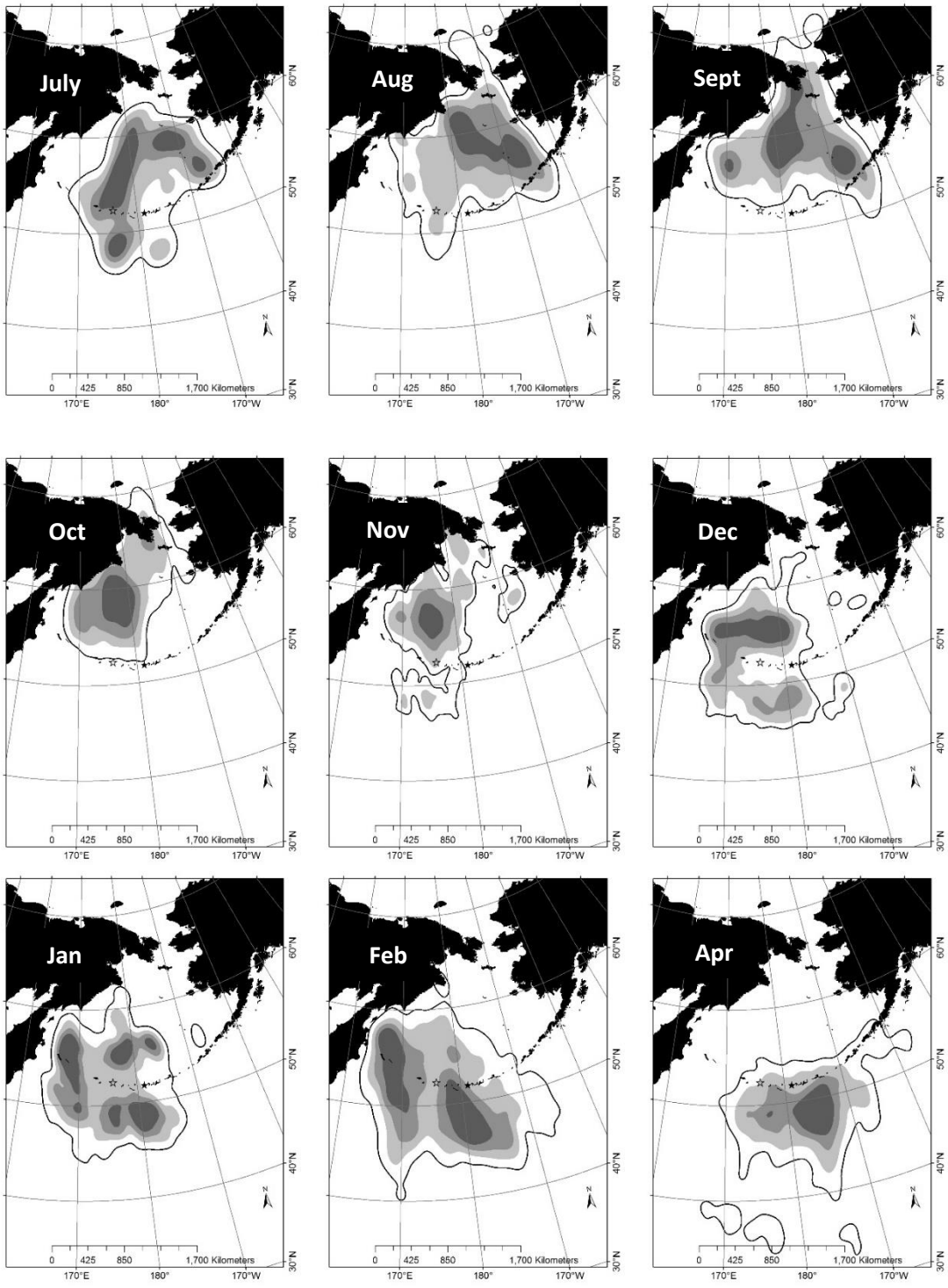

July
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Apr
60°N
50°N
40°N
30°N
0 425 850 1,700 Kilometers
170°E
180°
170°W

Figure 5-3. Monthly distribution maps for Parakeet Auklets (n=64). Percent volume contours derived from kernel density surfaces shown for 25% (dark gray), 50% (medium gray), 75% (light gray) and 90% (black outline) of location points. Note: July data include only the six individuals that left the colony before August; September distribution based on fewer data points (1 Sept – 9 Sept) due to the increased latitudinal error around the fall equinox. Colony locations marked with stars (Buldir: hollow star, Gareloi: filled star). Maps created in ArcGIS v.10.3 using a custom Albers equal area projection centered on the study area.

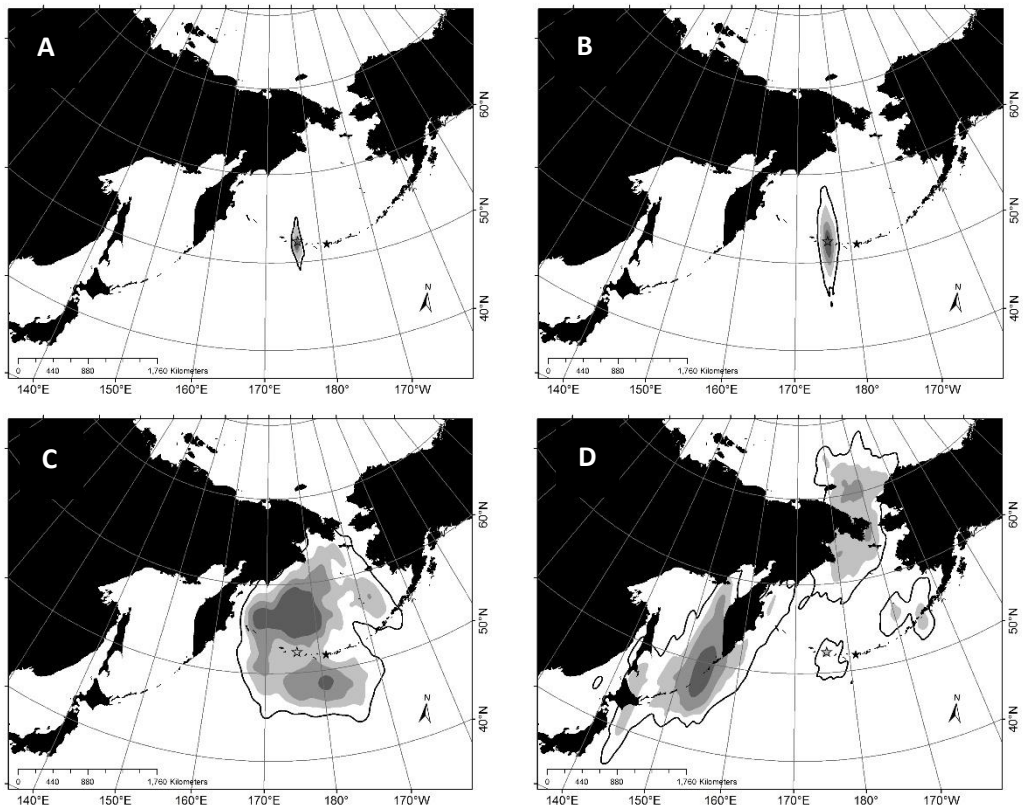
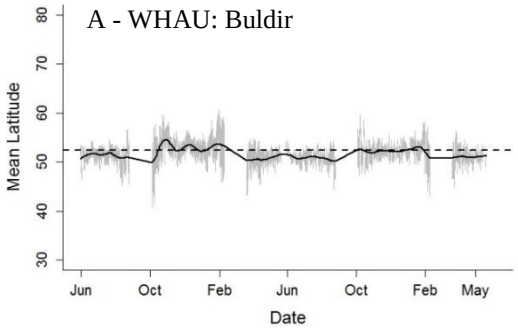
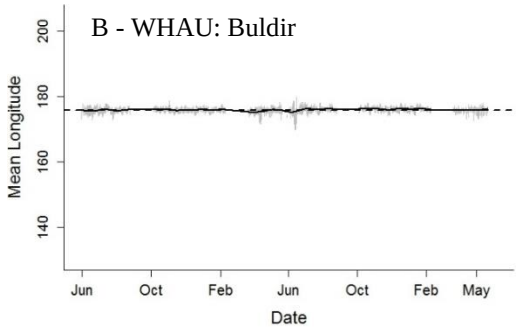
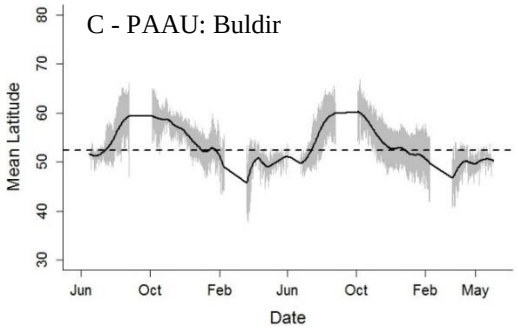
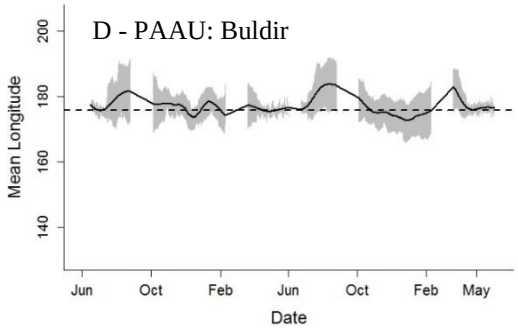


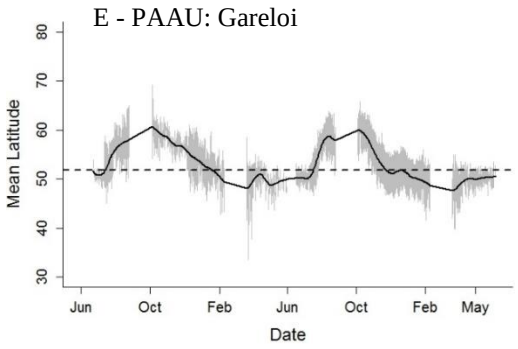
Figure 5-4. Data from stationary calibration tags on Buldir Island (A; n=5) provided as an estimate of position error for geolocation tags. Year-round distribution maps for Whiskered (B; n=17), Parakeet (C; n=64) and Crested auklets (D; n=98). Percent volume contours derived from kernel density surfaces shown for 25% (dark gray), 50% (medium gray), 75% (light gray) and 90% (black outline) of location points. Colony locations marked with stars (Buldir: hollow star, Gareloi: filled star). Maps created in ArcGIS v.10.3 using a custom Albers equal area projection centered on the study area.

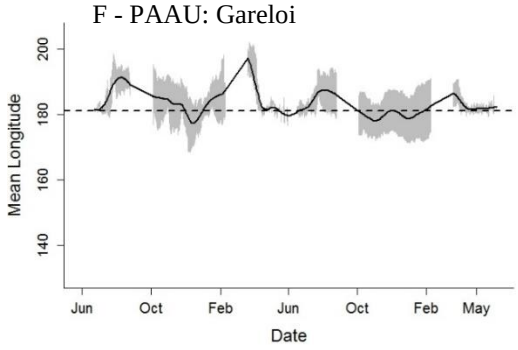

A - WHAU: Buldir
Mean Latitude
30
40
50
60
70
80
Jun
Oct
Feb
Jun
Oct
Feb
May
Date


B - WHAU: Buldir
Mean Longitude
140
160
180
200
Jun
Oct
Feb
Jun
Oct
Feb
May
Date


C - PAAU: Buldir
Mean Latitude
30
40
50
60
70
80
Jun
Oct
Feb
Jun
Oct
Feb
May
Date


D - PAAU: Buldir
Mean Longitude
140
160
180
200
Jun
Oct
Feb
Jun
Oct
Feb
May
Date


E - PAAU: Gareloi
Mean Latitude
30
40
50
60
70
80
Jun
Oct
Feb
Jun
Oct
Feb
May
Date


F - PAAU: Gareloi
Mean Longitude
140
160
180
200
Jun
Oct
Feb
Jun
Oct
Feb
May
Date

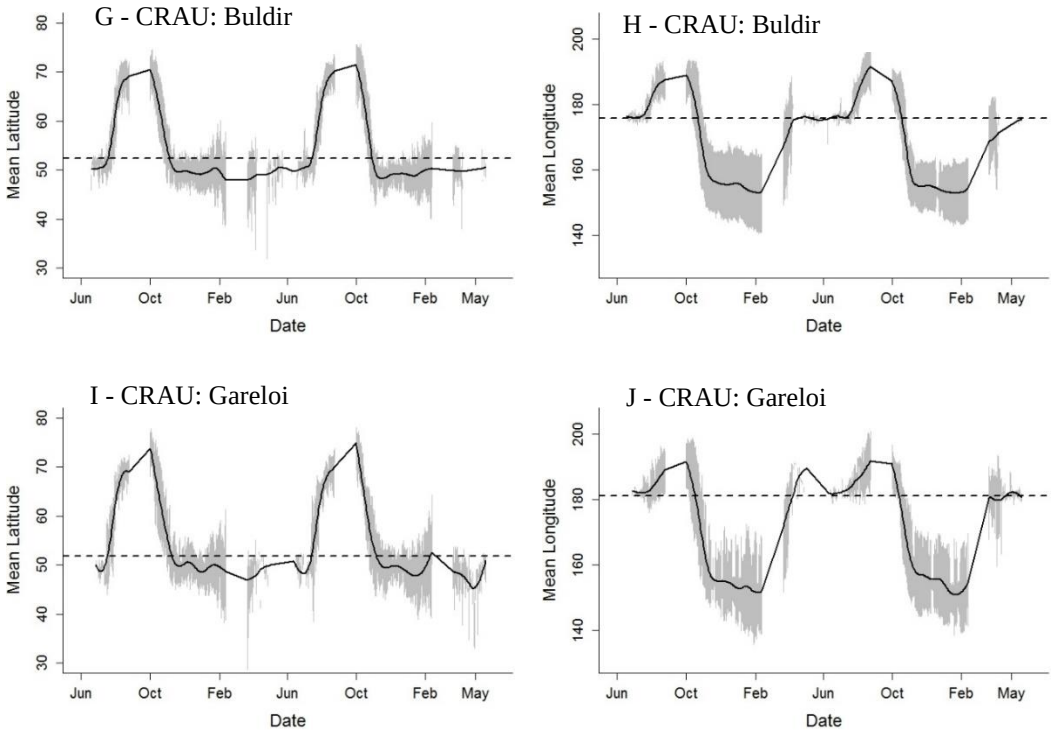


Figure 5-5. Daily average latitudes and longitudes (loess curve, span=0.1) during the non-breeding season (2013-2015) for Whiskered Auklets (WHAU; Buldir: A & B), Parakeet Auklets (PAAU; Buldir: C & D; Gareloi: E & F) and Crested Auklets (CRAU; Buldir: G & H; Gareloi: I & J). Vertical gray lines show daily standard deviations. Dashed horizontal lines show location of colony. Gaps in vertical lines indicate areas of missing data (breeding season, equinox) which were interpolated by the loess smoothing function.

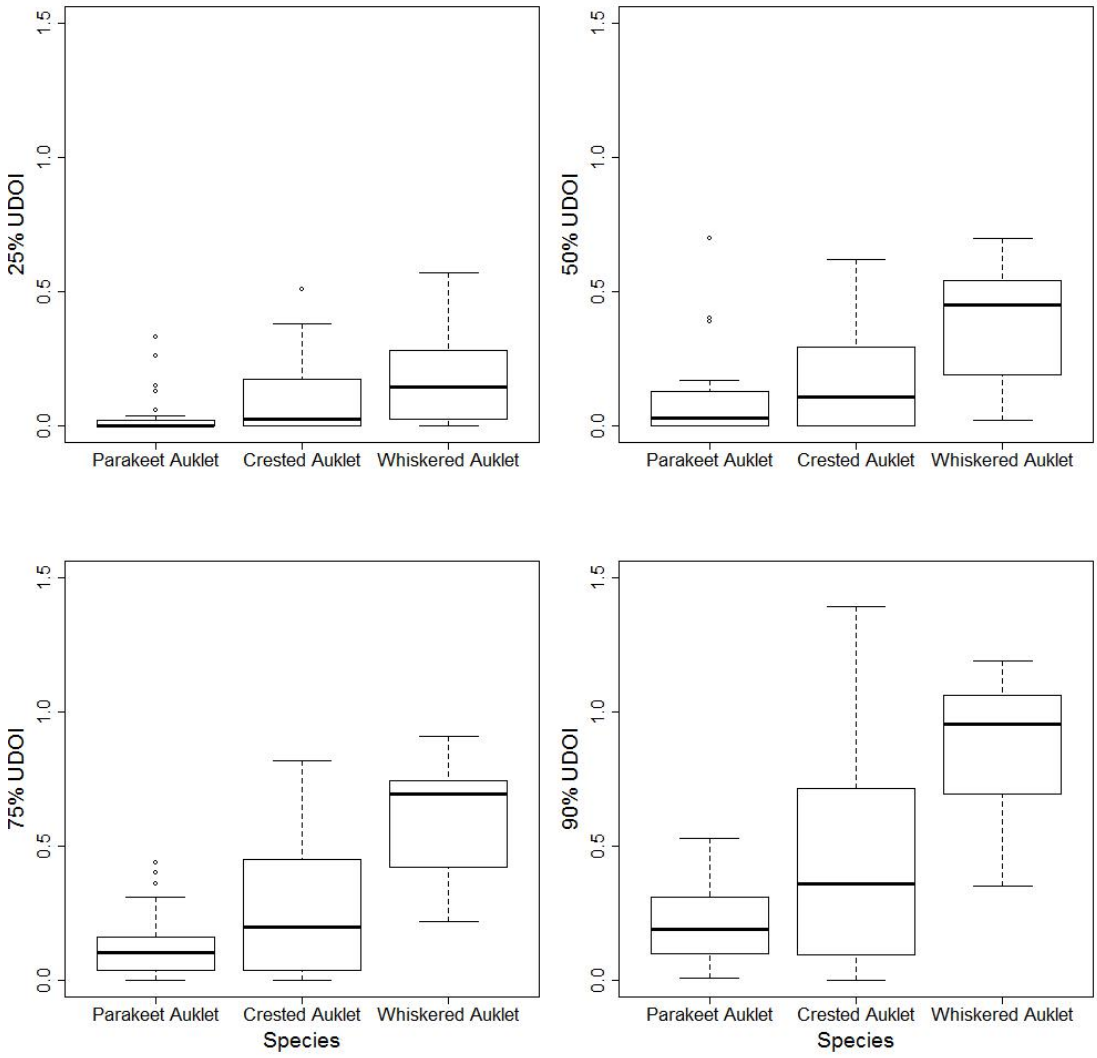
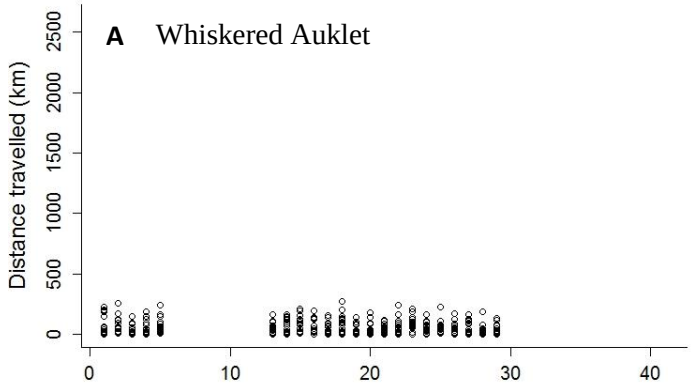
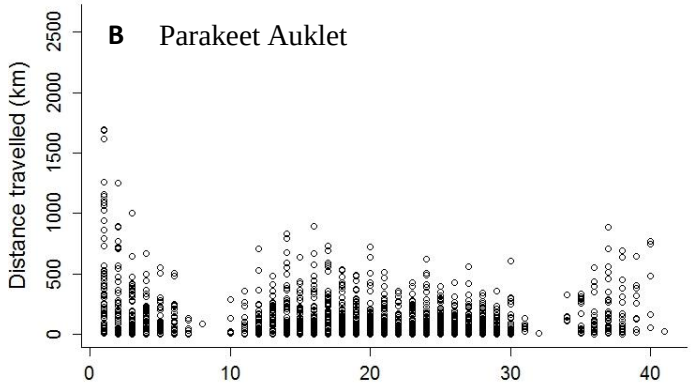


Figure 5-6. Comparison of random pairs of individuals (matched by species, island, and year) showed significantly higher overlap (UDOI) among Whiskered Auklets (n=20 pairs) than the other two species at all percent volume contours (VC). Crested Auklets (n=40 pairs) had significantly higher overlaps than Parakeet Auklets (n=30 pairs) at larger scales (75% and 90% VCs) only.


A Whiskered Auklet
Distance travelled (km)
0
500
1000
1500
2000
2500
0
10
20
30
40


B Parakeet Auklet
Distance travelled (km)
0
500
1000
1500
2000
2500
0
10
20
30
40

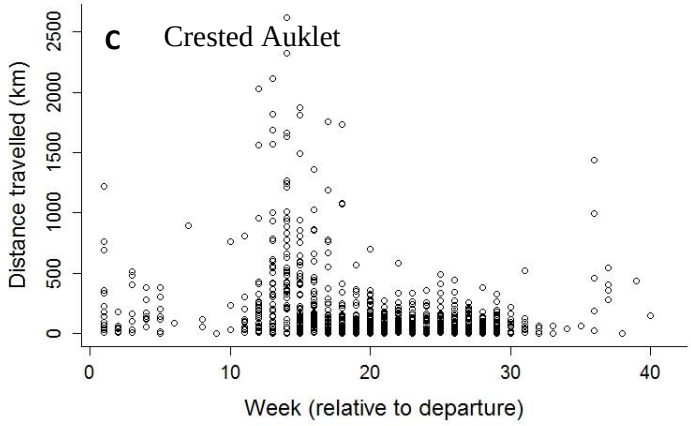

C Crested Auklet
Distance travelled (km)
0
500
1000
1500
2000
2500
0
10
20
30
40
Week (relative to departure)

Figure 5-7. Weekly travel distances for all individuals throughout the non-breeding season. Data are grouped by week, relative to the start of the non-breeding season (as defined in the text) to compensate for individual differences in migration timing.

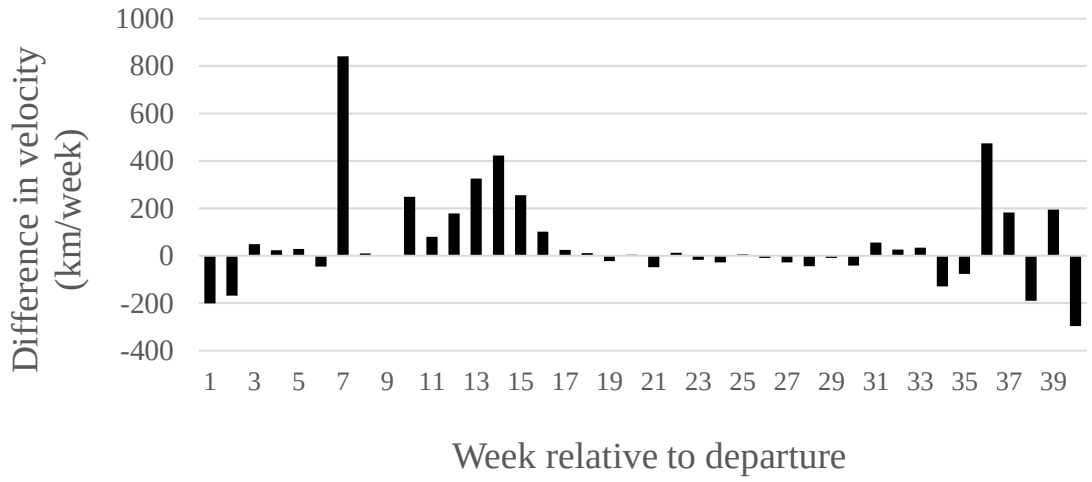


Figure 5-8. Difference in average weekly velocity (Crested Auklet – Parakeet Auklet) during the non-breeding season. I determined the non-breeding season for each individual based on date of departure from the vicinity of the breeding colony, and excluded individuals for which departure date could not be determined due to gaps in tracking data. I grouped the data by week, relative to the start of the non-breeding season (as defined in the text) to compensate for individual differences in migration timing.

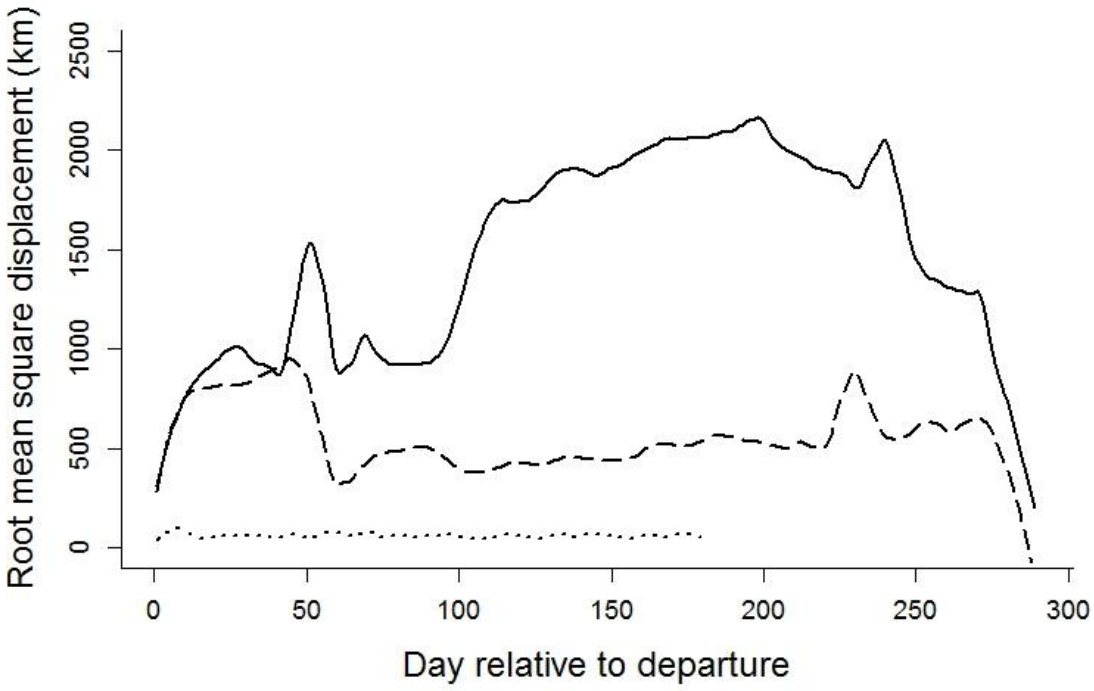


Figure 5-9. Average distance from colony (root mean square displacement; loess curve, span=0.1) over time during the non-breeding season for Whiskered (dotted line), Parakeet (dashed line), and Crested (solid line) auklets. I standardized data relative to departure date to compensate for individual differences in migration timing. Note: Whiskered Auklet dataset is shorter due to differences in the way the non-breeding season was defined.

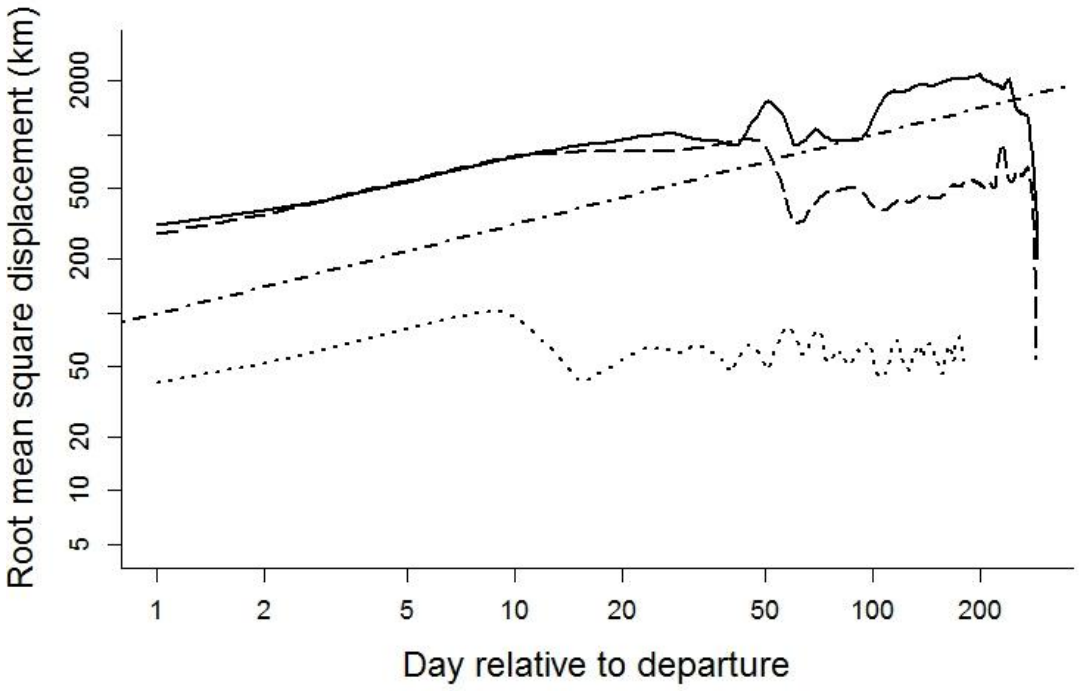


Figure 5-10. Average distance from colony (root mean square displacement; loess curve, span=0.1) over time during the non-breeding season for Whiskered (dotted line), Parakeet (dashed line), and Crested (solid line) auklets plotted on a log-log scale. Straight line of slope 0.5 represents diffusive movement; shallower slopes are sub-diffusive, steeper slopes are super-diffusive (Codling *et al.* 2008).

CHAPTER 6: SYNTHESIS

With this thesis, I aimed to investigate the full annual cycle of migration in a group of closely related seabirds (*Aethia* auklets), and apply the resulting tracking data to two tests of predictions from ecological theories. I began by experimentally evaluating potential negative effects of tracking tags on my study species in order to validate the interpretation of the resulting data (Chapter 2). I then used tracking data in a novel way to test predictions relating to food depletion around seabird colonies (Chapter 3). I used a combination of location data, behavioural data, and audio recordings at the colony to confirm year-round residence of one species at a North Pacific colony (Chapter 4). I also synthesized migratory theory into a continuum concept, and used the placement of three congeneric species on that continuum to develop and test predictions concerning migratory distance and average velocity, consistency of destination, distance travelled, and habitat use (Chapter 5).

The first step in any study relying on data from animal-borne devices should be a validation that the data produced by those devices is representative of normal behaviour, and has not been significantly altered by the presence of the device itself. Therefore, in Chapter 2, I conducted a controlled experiment to test for tag effects in two of my study species (Whiskered and Parakeet auklets), comparing adult return rate, reproductive success, and chick growth of tagged versus un-tagged birds (effects of tags on Crested Auklets are presented elsewhere; Robinson & Jones 2014, K. F. Robbins, unpublished data). Tags used in this study were well below generally accepted guidelines for seabird research (< 3% adult body mass; Phillips *et al.* 2003), but these guidelines were developed based on data for large Procellariiform species (albatrosses and petrels). Alcids

may be less tolerant of extra weight and/or drag than these species because their wings are adapted for underwater pursuit-diving (higher wing-loading) and so flight is energetically expensive (Pennycuick 1987, Obrecht *et al.* 1988, Vandenabeele *et al.* 2012). Studies of small alcids have shown negative effects of tags ≤ 3% body mass (Ackerman *et al.* 2004, Whidden *et al.* 2007, Elliott *et al.* 2010), and previous work on Crested Auklets (*A. cristatella*) showed strong effects of a tag (total attachment mass) weighing < 2% body mass on several aspects of reproduction and behavior (Robinson & Jones 2014), reinforcing the need for an assessment of potential tag effects in this study.

To complement my investigation of tag effects, I reviewed seabird tracking literature, focusing on how potential tag effects were evaluated or discussed. This review revealed a lack of consistency in reporting of tag effects. Among tracking studies, 52% made at least minimal measurements of effects, 11% made anecdotal statements that birds did not seem affected by tags, 6% cited previous research on their species, 8% cited the 3% guideline (Phillips *et al.* 2003) as evidence that measuring effects was not necessary; 23% made no mention of effects. I also found that, while the focus in tagging studies has generally been on relative tag mass, taxonomic group (as a proxy for various lifestyle-factors) was the best predictor of tag effects in the publications reviewed. Alcids were more than twice as likely to show negative effects of tags as other taxa, but, across taxa, the proportion of studies detecting negative effects was similar regardless of tag mass. This suggests that factors such as foraging style, or flight physiology/energetics may play a greater role than relative mass when predicting likely tag effects (Barron *et al.* 2010, Vandenabeele *et al.* 2012). The importance of hydrodynamic drag and details of

tag design and placement are also frequently mentioned, but rarely seriously considered (*e.g.*, Wilson *et al.* 1986)

Parakeet and Whiskered auklets showed varying tolerance for tags 0.8-1.8% body mass. Chicks of tagged Whiskered Auklets showed minor decreases in growth rates, but not fledging success, suggesting that an increased burden on the adults reduced their ability to provision offspring, but not enough to affect chick survival. I also found negative effects on adult condition and return rates of Whiskered Auklets in some years, but not others. Parakeet Auklets, on the other hand, showed very few negative effects of tagging, although, like Whiskered Auklets, the responses in some measures were variable across years. The strong effect on Whiskered Auklet return rate in one year of the study was surprising. Whiskered Auklets are the smallest species in this study (tags represent a larger percentage of body mass), but, because they do not make long foraging or migratory flights (Byrd & Gibson 1980, Chapter 4), I expected a lower impact of additional mass for these birds than for more highly migratory species. However, the winter of 2014-2015 was particularly harsh in the Bering Sea, and Whiskered Auklet survival has been shown to vary with local winter conditions, with higher mortality in stormy winters (Jones *et al.* 2007). The burden of tags may have exacerbated this effect, if birds that could normally compensate were not able to do so when already operating near their metabolic limit (Croll and McLaren 1993, Humphreys *et al.* 2007).

Overall, I found that Parakeet Auklets showed a good tolerance for the tags used in this study (1-2g), while 1g tags may be too large for Whiskered Auklets to bear without experiencing considerable stress, a result that has been taken into account in

subsequent interpretation of tracking data. Perhaps more importantly, my data suggest that the effects of tags are not necessarily consistent. Effects can vary significantly among sexes, among closely related species of similar size, and among years within the same species at the same colony (see Weiser *et al.* 2016 for similar results in shorebirds). Given this variation, it is difficult to justify simply citing previous research when evaluating the potential for tag effects in any new study. Broadly applied guidelines are also problematic. This study and others have demonstrated negative effects on reproduction, behavior, and return rates in alcids of tags well below the 3% guideline typically cited (e.g. Ackerman *et al.* 2004, Paredes *et al.* 2005, Robinson & Jones 2014). These results suggest that different species are affected differently by tags and that guidelines, even those that are well-established for one group, should not be applied universally without validation (Vandenabeele *et al.* 2012). I encourage researchers to incorporate at least minimal effects monitoring in all tracking studies. Depending on the duration of researcher presence and the accessibility of the site, many studies could incorporate a basic assessment of reproductive success and/or adult return rates relative to control birds with minimal additional effort and disturbance. Including effects studies in tracking projects would provide a measure of confidence for their interpretation, and allow for weighing the validity of the resulting data.

In Chapter 3, I used tracking data in a novel way to test predictions relating to food depletion around seabird colonies ('Ashmole's Halo'; Birt *et al.* 1987). I discussed the possibility of food depletion as a driver of migration in planktivorous species. Ashmole (1963) postulated that any density-dependent effects regulating seabird

populations operate at the colony, and most likely involve the availability of food (Ashmole 1971). Specifically, Ashmole (1963) proposed that the concentration of breeding individuals with high nutritional needs in a limited area will lead to a near-colony reduction in the availability of food. If so, the resulting increase in foraging effort required could serve as a proximate cue triggering post-breeding migration in some species. Ashmole's hypothesis has been difficult to test directly. Indirect tests have focused on piscivorous seabirds, and have largely ignored the influence of advective resupply in replenishing the local prey population (Bourne 1983, Schneider *et al.* 1992). This resupply is likely to be especially important for planktivorous species, since the lateral distribution of zooplankton, unlike most fish species, is determined mainly by passive transport, and concentration by features of the local oceanography (Mackas *et al.* 1985, Schneider 1991, Spear *et al.* 2001).

To investigate the role of food depletion during the breeding season at large colonies of planktivorous seabirds, I looked at how three species of *Aethia* auklets differ in their response to being released (by the completion of breeding) from the constraint of foraging near the colony. I combined monitoring of individual reproductive timing with tracking data obtained from geolocation tags deployed on those same individuals (to determine the date of colony departure). If food is an important limiting factor at the colony (whether due to food depletion, or interference competition), individuals should leave as soon as possible once the current breeding effort is completed. My data did not support this prediction. Whiskered Auklets (which, with the highest metabolic demands, should have been under the most pressure to seek out the best food sources) did not

migrate at all. Instead, they remained resident at or near the colony all winter (discussed in more detail in Chapter 4). Parakeet and Crested auklets did migrate, but did not leave as soon as breeding was completed, with lag times up to 30 days after cessation of breeding. Early failed breeders left before later breeders, but not as soon as possible. In contrast, a tracking study of Black-browed Albatrosses showed that birds that failed early in the season departed for their winter feeding grounds months before late failures and successful birds (Phillips *et al.* 2005), suggesting that prey depletion may have been a factor at that colony, or at least that there was a large advantage in relocating to their highly productive wintering area as soon as possible. In the case of the auklet colonies in this study, it is more likely that the local current systems are providing a reliable influx of planktonic prey (advective resupply; Bourne 1983, Schneider *et al.* 1992). More studies of this nature will be needed to determine if there are consistent differences among planktivorous and piscivorous species.

My results do not support the hypothesis that reduced food availability acts as a proximate trigger of migration in this system, given the long lag time observed. However, they do indicate interesting differences in migratory strategy. Timing data are consistent with the placement of these three closely related species at different points on a continuum of migratory behaviour (a concept explored in more detail in Chapter 5), ranging from year-round residence in the Whiskered Auklet (confirmed in Chapter 4 using tracking and behavioural data), to facultative migration in the Parakeet Auklet, and obligate migration in the Crested Auklet. Obligate migrations are characterized by a higher degree of consistency in timing (and other aspects) than facultative migrations

(Newton 2012), a difference that is reflected in Crested and Parakeet auklet departure data. Crested Auklets had a more synchronized migration departure than Parakeet Auklets. The decrease in lag times as the breeding season progressed also suggests that there is an optimal window of departure for Crested Auklets late in the breeding season (Alerstam 1978), possibly under selection to maximize exploitation of productive seasonal foraging habitat in the Chukchi Sea before the southward spread of the ice pack (Gall *et al.* 2013, Kuletz *et al.* 2015). Parakeet Auklets had lower departure synchrony, consistent with a more facultative/dispersive migration (Newton 2012), with little evidence of a strong internal clock regulating departure times, or pressure for a rapid departure from the colony. Migration timing in these species likely has more to do with conditions at the wintering area than those at the breeding site. Crested Auklet foraging behaviours seem to be adapted to finding and exploiting spatially predictable aggregations of prey (Chapter 5), in this case the Chukchi Sea, a time-limited habitat accessible only until the seasonal advance of the ice pack in October/November. The more generalist Parakeet Auklets can afford to be more flexible in the timing (and destination) of their migration, following no pre-determined route and making individual decisions based on their current condition and changes in the local environment.

After confirming in Chapter 3 that Whiskered Auklets breeding on Buldir Island did not leave the vicinity of the colony, I explored the winter residence of Whiskered Auklets in more detail in Chapter 4. This species has been named a species of conservation concern, and is considered especially vulnerable to oil spills, introduced mammalian predators, and other threats due to its restricted distribution and its year-

round presence in Aleutian passes (Troy & Bradstreet 1991, Troy 1991, Williams *et al.* 2003, NPRB 2005). There have been anecdotal reports for many years of adults and juveniles returning to the islands periodically in winter (*e.g.*, Stejneger 1885, Murie 1936, Byrd & Gibson 1980, Zubakin & Konyukhov 2001), and ship-based surveys show that Whiskered Auklet winter distribution at sea is largely restricted to areas within a few kilometres of the Aleutian Islands (Byrd & Williams 1993, NPPSD 2015). However, winter survey coverage is limited (NPPSD 2015), and provides no information as to the colony-of-origin of sighted birds. I investigated the wintering strategy of Whiskered Auklets breeding at Buldir Island, using a combination of tracking data (to map winter distribution), behavioural data (sea water immersion sensors on tags, to measure daily activity patterns), and year-round audio recordings at the colony (to confirm presence near breeding sites).

My data show that Whiskered Auklets breeding at Buldir are non-migratory. Tracked individuals were distributed near the island during the non-breeding season, and audio recordings confirmed their presence at the colony site itself from at least March to October. Unlike their congeners, Whiskered Auklets roosted on land at night year-round, except for occasional trips to sea during full moon periods, presumably to forage when there was sufficient light and/or stronger tidal currents (Jones *et al.* 2002, Phalan *et al.* 2007, Paredes *et al.* 2008, Regular et al. 2011). Whiskered Auklets' winter roosting behaviour might be an adaptation to reduce metabolic costs by avoiding cold water when not foraging. However, this behaviour also greatly increases their vulnerability to

introduced mammalian predators, especially during the non-breeding season when few other prey species remain (Williams *et al.* 2003).

I cannot make firm conclusions about the species as a whole based on data from one island. Colonies at the northern limits of the Whiskered Auklet's range in the Sea of Okhotsk are surrounded by pack ice in winter (Gaston and Jones 1998), possibly necessitating some form of migration in those populations. However, winter residence at most colonies (leading to a lack of mixing among populations) would be consistent with the clinal variation in body size and ornamentation observed in the Whiskered Auklet (Byrd and Williams 1993), and the stronger genetic differentiation among Whiskered Auklet colonies compared to the more mobile Crested Auklet (Pshenichnikova *et al.* 2015, 2017). Winter residence at the breeding site is uncommon in seabirds (Bridge 2006), but it could be energetically favorable to remain near the colony if sufficient prey is available to sustain the population. Whiskered Auklets specialize in feeding at tide rips close to the island (Byrd & Gibson 1980, Herter 1991, Byrd & Williams 1993), which operate year-round, providing an accessible source of food near the surface (Holm & Burger 2002, Ladd *et al.* 2005). The limited data available on winter diet suggest that Whiskered Auklets in the western Bering Sea (Bering Island) switch from the copepods preferred during the breeding season (Day & Byrd 1989) to eating mainly gammarid amphipods (Stejneger 1885), which do not provide enough nutritional content to successfully raise chicks (Bédard 1969), but may be sufficient during the non-breeding season when energetic demands are reduced. Winter land roosting may serve to further

reduce their energetic requirements during the winter by avoiding the metabolic costs of resting in cold water at night.

In Chapter 5, I provided the first description of migration and winter distribution of Parakeet Auklets. I then built on results from previous chapters to synthesize migratory theory into a continuum concept, which I used to develop and test predictions concerning migratory distance and velocity, consistency of destination, distance travelled, and habitat use. I proposed the placement of three *Aethia* auklet species on a continuum of migratory behaviour from long-distance, directed (LDD) migration (Crested Auklets) to intermediate migration (Parakeet Auklets) to residence (Whiskered Auklets), based on *a priori* knowledge about their ecology, behaviour and morphology. My migration continuum (Fig. 5-1) combines several inter-related aspects of migration, including distance travelled (residence, short-distance dispersive migration, long-distance migration), type of migration (obligate, facultative), and type of movement used during migration (sub-diffusive, super-diffusive, ballistic).

Overall, tracking data supported predictions based on a ranking of these three species of *Aethia* auklets on a continuum of migratory behaviour from residence (Whiskered Auklets) to intermediate migration (Parakeet Auklets) to LDD migration (Crested Auklets). Crested Auklets travelled furthest on their migration (see also Robinson 2015, KF Robbins, unpublished data), followed by Parakeet Auklets, then Whiskered Auklets. Crested Auklets showed greater individual consistency of migration timing (Chapter 3), and space use than Parakeet Auklets, both at the individual and at the species level. I also found distinct differences in relative habitat use between Crested and

Parakeet auklets, with Crested Auklets more likely to be found in shallower shelf waters, and Parakeet Auklets making greater use of deep basin regions. Crested Auklets were more strongly associated with productive northern areas like the Chukchi Sea during the ice-free period (August-October) before moving south to their secondary wintering area, the timing of which coincides with the southward progression of the ice pack (KF Robbins, unpublished data). Although most data matched well with my predictions, some did not. Facultative migrants are expected to have more variable migrations, and are more likely to segregate during the winter by sex or by colony (Newton 2012). However, I did not find Parakeet Auklets to have higher variance than Crested Auklets in most of my distance measures (although this may be explained by a small number of individual Crested Auklets that diverged from the majority and used a different wintering area to the east). I also did not find that Parakeet Auklets showed significant differences in wintering area between sexes or between colonies. However, despite being more likely to show such segregation, not all facultative migrants must do so, and so an absence of difference does not necessarily indicate an error of classification. I had also predicted that, due to their use of time-limited near-ice habitat (now confirmed by tracking data), Crested Auklets would show characteristics of a time-minimizing post-breeding migration (as defined by optimal migration theory; Alerstam & Lindström 1990), but I found no evidence to support this.

Despite their close relationship, and similar breeding biology, the three congeneric species studied here used very different strategies for survival during the non-breeding season. These differences are likely driven by differences in diet and foraging

behaviour. Whiskered Auklets (from Buldir Island, and likely other southern colonies) are residents near the breeding site, and roost on land at night year-round (Chapter 4), an uncommon strategy in seabirds (Bridge 2006) that may be enabled by their specialized feeding in tide rips close to their colonies, which provide a reliable and accessible source of prey all year (Day & Byrd 1989, Holm & Burger 2002, Ladd *et al.* 2005). Residence can also provide advantages in terms of an earlier start to the breeding season (O'Connor *et al.* 1984). Whiskered Auklets have the longest chick rearing period of the *Aethia* auklets. An early start to breeding may be necessary in order for the chicks to fledge before the end of the breeding season and could contribute to Whiskered Auklets' non-migratory strategy. Crested Auklets undertook a loop-type LDD migration to two distinct wintering areas before returning to the colony (KF Robbins, unpublished data). Their high degree of consistency in habitat use (high overlap at the individual, colony, and species levels), and their aggregation in areas where a combination of currents and topography result in concentrations of accessible prey, suggest that Crested Auklet foraging behaviours are adapted to finding and exploiting spatially predictable aggregations of prey in regions such as the Chukchi Sea and the Oyashio Current region (their two main wintering areas, which are used by many seabirds; e.g. Suryan *et al.* 2006, Rayner *et al.* 2011, Kuletz *et al.* 2015). Parakeet Auklets have a more generalist diet than other auklets (Hunt *et al.* 1998), including large amounts of gelatinous zooplankton and the hyperiid amphipods that are associated with jellyfish (Harrison 1984, Schneider *et al.* 1986, Hunt *et al.* 1993, 1998, Mudge & Pietzrak 2015). These dietary/foraging differences could allow Parakeet Auklets to subsist in less productive

regions, such as the deep waters of the Aleutian Basin, an important wintering area for all individuals tracked in this study, but not generally considered a productive hotspot for winter seabird abundance (Sydeman *et al.* 2010, NPPSD 2015).

I took advantage of recent developments in lightweight and inexpensive geolocation tracking technology (DeLong *et al.* 1992, Wakefield *et al.* 2009, Wilson & Vandenabeele 2012) that allow for deployment of tags on smaller species, and at larger sample sizes for more robust mapping of winter ranges and greater statistical power for testing predictions from theory. These tags have lower accuracy than larger, more expensive options (Wakefield *et al.* 2009), and are archival, requiring that tagged birds be recaptured after deployment to recover the data. These burrow/crevice nesting seabirds have proven to be good candidates for this type of archival tag, with a high degree of nest site fidelity leading to generally high tag recovery rates (mean in this study: 61%, range: 24-79%). I was also careful to limit my investigation to large scale questions (tag accuracy when deployed on birds in this study was likely ~200km; see Chapter 4), and to use methods that do not rely on the accuracy of individual location points. I used weekly, instead of daily velocities, and used monthly percent volume contours (or the centroids of their distributions) as data points for most measurements, instead of using the twice-daily location points provided by the tags. While each individual location may have low accuracy, when combined into a density surface we can be reasonably confident that the aggregate approximates the true spatial use of the bird (Marzluff *et al.* 2004, Millspaugh *et al.* 2006, Hooten *et al.* 2013).

This study was limited by the number of colonies that could be visited. Although my samples sizes (in terms of number of individuals tracked) are substantial compared to most tracking studies, I cannot necessarily generalize about species as a whole based on data from one or two colonies. Whiskered Auklets breeding in the Sea of Okhotsk are surrounded by pack ice in winter (Gaston and Jones 1998), possibly resulting in some form of migration in those populations. There is also evidence to suggest that eastern Aleutian colonies of Parakeet and Crested auklets have different wintering areas than those from the western Aleutian colonies studied here. Unimak Pass in the eastern Aleutians is host to large numbers of Crested Auklets during winter (Troy & Bradstreet 1991, Renner *et al.* 2008), despite being visited by only a small minority of our tagged birds (KF Robbins unpublished data), and Parakeet Auklets are frequently observed offshore of Washington and California (Jones *et al.* 2001), suggesting that eastern populations may have a more coastal southward migration. Further investigation will be required to determine if the general interspecific patterns observed in my data will hold true across regions.

In addition to the theoretical questions addressed, this thesis provided a number of descriptive results, which are important in the context of seabird conservation. I have produced the first winter distribution maps based on tracking data for Whiskered and Parakeet auklets (KF Robbins provided the Crested Auklet data used for comparison). Previous assumptions about winter range in Parakeet Auklets based on ship-based survey data and other sightings have proven to be inaccurate and/or incomplete (Chapter 4, Chapter 5, Schacter & Robbins 2016), over-estimating the importance of more easily

surveyed coastal regions and missing the widespread use of the Aleutian Basin. Overall, Whiskered Auklet distribution was well-represented by survey data (Byrd & Williams 1993, Schacter & Robbins 2016), but the extent of winter residence could not be determined without the knowledge of colony-of-origin provided by tracking data. Accurate information about the winter range and behaviour of these species allows us to identify areas of potential conflict with human activities. Whiskered Auklets were already considered a species of special concern due to their year-round presence near the Aleutian Islands and in passes with high shipping traffic (NPRB 2005). I have shown that the use of land by adults for roosting throughout the non-breeding season is even more extensive than expected, making them especially vulnerable to introduced mammalian predators (Williams *et al.* 2003). Large numbers of Crested (and to a lesser extent, Parakeet) Auklets were known to make use of Chukchi Sea habitat in late summer and early autumn (Gall *et al.* 2013, Kuletz *et al.* 2015), although these have been assumed to be mostly birds from northern Bering Sea colonies. Tracking data now show that this region is also a major wintering area for at least two southern colonies (Buldir and Gareloi islands). As the ice-free season becomes longer and there are increased opportunities for shipping and oil exploration in the Chukchi Sea, any negative impact on the wintering auklets will be felt by a larger proportion of the population than previously realized. Crested Auklets may be particularly vulnerable due to their relative lack of flexibility (Chapter 3, Chapter 5), and their susceptibility to light attraction by vessels and platforms (Dick & Donaldson 1978, NPRB 2005).

The different migration strategies that I have shown in these species also suggest different management approaches. The migratory continuum presented in Chapter 5 matches well with the degree of genetic structure in auklet species. Recent work has shown a high degree of genetic and phenotypic differentiation among Whiskered Auklet colonies (Pshenichnikova *et al.*, 2017), intermediate levels in Parakeet Auklets (O. S. Pshenichnikova, unpublished data), and very little in Crested Auklets (Pshenichnikova *et al.* 2015), suggesting that the non-migratory Whiskered Auklet with limited genetic connectivity among colonies might be better managed as separate populations, while Crested Auklets likely form larger regional units.

Researchers have just begun to explore the potential of tracking data as a resource to test theories of migration (e.g. Pérez *et al.* 2014, Reynolds *et al.* 2015), foraging ecology (e.g. Hinke *et al.* 2015, Wakefield *et al.* 2015), carry-over effects (e.g. Fayet *et al.* 2016), etc. Migration behaviour, in particular, has been difficult to study directly before the advent of tracking technology, relying largely on mathematical modelling, combined with empirical data from banding studies, flight energetics (Alerstam & Hedenström 1998, Alerstam 2001, Newton 2006), and field research at known stopover sites when accessible (Lindström & Alerstam 1992, Creswell 1994), something rarely possible for seabirds. This has changed in recent years, with tracking data being used to test optimal migration predictions about the use of wind by migrating birds (e.g. Åkesson & Hedenström 2000, Thorup *et al.* 2003, González-Solis *et al.* 2009, Fifield et al. 2014). I have shown that it is possible to develop and test hypotheses about population regulation (Chapter 3) and migration dynamics (Chapter 5) using Lagrangian data from tracking

devices instead of (or in addition to) the usual Eulerian data available from surveys of seabird distribution at sea. I have also used this data to synthesize migration theory into a continuum concept with interesting potential applications for further research. The integration of migration theory with an advection-diffusion approach to migration dynamics (Kölzsch & Blasius 2008, Codling *et al.* 2008) would be of great interest (see discussion below), as would an extension of migratory theory to form more specific predictions concerning distribution and dynamics of seabirds away from colonies and stopover sites.

My data show inconsistencies with some of the predictions of optimal migration theory. These inconsistencies highlight issues with the application of optimal migration models to seabirds. Optimal migration models are based on a stepping-stone construction (Alerstam & Hedenström 1998, Åkesson & Hedenström 2007), with travel between discrete stopover sites and foraging areas, crossing 'barriers' where foraging is impossible or much reduced. While these models perform well for landbirds and shorebirds, the marine environment is very different. High-quality foraging habitat at sea is heterogeneously distributed (Southwood 1977, Weimerskirch 2007), especially for specialists like Crested Auklets, but there are few true barriers that must be crossed without foraging, as there are in terrestrial and coastal systems. In fact, many seabirds likely make at least partial use of a 'fly-and-forage' strategy (e.g. Strandberg & Alerstam 2007, Dias *et al.* 2012). Given the limited information available about the details of winter foraging behaviour for most seabird species, it is difficult to determine when these models are appropriate. In many cases, an advection-diffusion model may be a better

approach for migration in marine habitats. These models (based on a type of biased random walk) incorporate diffusive movement through space and directional bias to/from breeding and wintering areas (Okubo 1980, Codling *et al.* 2008, Codling *et al.* 2010). Advection-diffusion models (also known as drift-diffusion models) have been used to investigate migration and dispersal in several fish species (e.g. Sibert *et al.* 1999, Zabel 2002, Magnússon *et al.* 2005). An application of these techniques to seabird movements would make an interesting comparison with existing models.

Future work on *Aethia* auklets will be necessary to get a full picture of winter habitat use and migration behaviours in these species. Specifically we will need to obtain tracking data from a wider selection of colonies, ideally representative of the entire breeding range (including Eastern Aleutians, Sea of Okhotsk, and Bering Sea colonies). There is also a lack of migration/wintering information for the remaining member of the *Aethia* genus, the Least Auklet (*Aethia pusilla*; ~80g). Tags currently available are still likely too large for deployment on this smallest member of the genus, but the technology is developing rapidly. Tracking data for this species would provide an excellent opportunity for a test of the migration continuum developed in Chapter 5. Least Auklet foraging habitat shares many characteristics with that preferred by Crested Auklets, based around oceanographic features that maximize the abundance and accessibility of prey (Hunt & Harrison 1990, Hunt *et al.* 1993, Gall *et al.* 2013). However, their foraging distributions are less tightly clumped than those of Crested Auklets (Bédard 1969). Ship-based survey data show a distribution broadly similar to Crested Auklets (NPPSD 2015), but they use northern Chukchi Sea habitat in smaller numbers than Crested Auklets

(though greater than Parakeet Auklets; Gall *et al.* 2013), and do not occur at sea in such dense concentrations (Bond *et al.* 2013). The lack of pronounced geographic variation in body size and other characteristics also suggests a fairly high degree of population mixing similar to Crested Auklets (Bond *et al.* 2013). Based on these characteristics, I would hypothesize the placement of Least Auklets between Parakeet (intermediate migrants) and Crested (LDD migrants) auklets, but closer to Crested Auklets.

The congeneric species studied here, with their different strategies for survival in the same environment during the non-breeding season, have great potential as a model system for comparative studies investigating other aspects of migration theory. Similarly sympatric species groups are increasingly being used to address theoretical questions, most commonly regarding spatial/ecological segregation during the non-breeding season (e.g. Phillips *et al.* 2007, Orben *et al.* 2014, McFarlane-Tranquilla *et al.* 2015). There is still much untapped potential in tracking data (especially in comparative systems) to provide empirical tests of predictions derived from ecological theory. Tracking data are often archived in publicly accessible databases (e.g. Movebank) or available through public funding agencies (e.g. North Pacific Research Board). These data provide a great opportunity to look at more in depth questions (without conducting additional field work), but are currently underutilized.

I have shown that tracking data can be used to address theory and play an important role in synthesizing concepts. Such synthesis is necessary to put conservation biology on a sound scientific basis. The application of more data from tracking studies to

theoretical questions can push science forward, and advance conservation goals, both through direct management applications of data, and contribution to ecological theory.

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APPENDICES

Appendix 2-1. List of studies included in literature review of tag effects.

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Appendix 5-1. Details of additional statistical tests that are summarized in the text. Significance presented after F-values (*** p<0.001, ** p<0.01, * p<0.05, ł p<0.1), followed, when relevant, by a letter showing the species/sex (C = Crested Auklet, P = Parakeet Auklet, M = male) located closest to the ice-edge, or with greater variance in distance measures. VC = Volume contour.

	Effect	Month	90% VC	75% VC	50% VC	25% VC
Distance to ice-edge	Species	August	$F_{1,78}$ = 60.8 *** C	$F_{1,78}$ = 73.1 *** C	$F_{1,78}$ = 73.4 *** C	$F_{1,78}$ = 65.6 *** C
	Species	*Sex*	$F_{1,78}$ = 3.7 ł M	$F_{1,78}$ = 4.8 * M	$F_{1,78}$ = 6.8 * M	$F_{1,78}$ = 7.6 **M
	Species	October	$F_{1,103}$ = 122 *** C	$F_{1,103}$ = 126 *** C	$F_{1,103}$ = 132 *** C	$F_{1,103}$ = 120 *** C
	Species	November	$F_{1,140}$ = 16.9 *** P	$F_{1,140}$ = 27.2 *** P	$F_{1,140}$ = 45.9 *** P	$F_{1,140}$ = 49.4 *** P
	Species	December	$F_{1,144}$ = 185 *** P	$F_{1,144}$ = 188 *** P	$F_{1,144}$ = 189 *** P	$F_{1,144}$ = 186 *** P
	Species	January	$F_{1,137}$ = 112 *** P	$F_{1,137}$ = 112 *** P	$F_{1,137}$ = 110 *** P	$F_{1,137}$ = 107 *** P
	Species	February	$F_{1,130}$ = 55 *** P	$F_{1,130}$ = 59 *** P	$F_{1,130}$ = 62.2 *** P	$F_{1,130}$ = 60.7 *** P
	Species	April	$F_{1,48}$ = 1.7	$F_{1,48}$ = 0.7	$F_{1,48}$ = 0.5	$F_{1,48}$ = 0.4
Variance in distance to ice-edge	Species	August	$F_{62,23}$ = 2.1 * P	$F_{62,23}$ = 2.1 ł P	$F_{62,23}$ = 1.6	$F_{62,23}$ = 1.3
	Species	October	$F_{47,62}$ = 1.4	$F_{47,62}$ = 1.5	$F_{47,62}$ = 1.2	$F_{47,62}$ = 1.0
	Species	November	$F_{89,63}$ = 1.9 ** C	$F_{89,63}$ = 2.2 ** C	$F_{89,63}$ = 2.8 *** C	$F_{89,63}$ = 3.1 *** C
	Species	December	$F_{93,63}$ = 1.4	$F_{93,63}$ = 1.4	$F_{93,63}$ = 1.3	$F_{93,63}$ = 1.2
	Species	January	$F_{87,63}$ = 1.3	$F_{87,63}$ = 1.3	$F_{87,63}$ = 1.4	$F_{87,63}$ = 1.3
	Species	February	$F_{78,63}$ = 3.1 *** C	$F_{78,63}$ = 3.1 *** C	$F_{78,63}$ = 2.9 *** C	$F_{78,63}$ = 2.7 *** C
	Species	April	$F_{6,48}$ = 2.0	$F_{6,48}$ = 2.4 ł C	$F_{6,48}$ = 1.9	$F_{6,48}$ = 1.3

	Effect	Month	90% VC	75% VC	50% VC	25% VC
Variance in distance to island	Species	August	$F_{62,23}$ = 1.5	$F_{62,23}$ = 1.3	$F_{62,23}$ = 1.0	$F_{62,23}$ = 1.2
	Species	October	$F_{47,62}$ = 1.6 ł C	$F_{47,62}$ = 1.5	$F_{47,62}$ = 1.5	$F_{47,62}$ = 1.4
	Species	November	$F_{89,63}$ = 1.1	$F_{89,63}$ = 1.3	$F_{89,63}$ = 1.5 ł C	$F_{89,63}$ = 1.1
	Species	December	$F_{93,63}$ = 2.5 *** C	$F_{93,63}$ = 2.5 *** C	$F_{93,63}$ = 2.4 *** C	$F_{93,63}$ = 2.1 *** C
	Species	January	$F_{87,63}$ = 4.6 *** C	$F_{87,63}$ = 4.8 *** C	$F_{87,63}$ = 5.2 *** C	$F_{87,63}$ = 5.6 *** C
	Species	February	$F_{78,63}$ = 4.1 *** C	$F_{78,63}$ = 4.2 *** C	$F_{78,63}$ = 4.5 *** C	$F_{78,63}$ = 5.0 *** C
	Species	April	$F_{6,48}$ = 1.4	$F_{6,48}$ = 2.1	$F_{6,48}$ = 1.9	$F_{6,48}$ = 1.2
Relative habitat use (percent overlap with bathymetry zone)	Species x Month x Zone		$F_{28,4052}$ = 21.5 ***	$F_{28,4052}$ = 18.6 ***	$F_{28,4052}$ = 14.5 ***	$F_{28,4052}$ = 10.8 ***
	Species x Zone	August	$F_{4,407}$ = 15.1 ***	$F_{4,407}$ = 20.5 ***	$F_{4,407}$ = 21.6 ***	$F_{4.407}$ = 19.8 ***
		October	$F_{4,532}$ = 60.9 ***	$F_{4,532}$ = 56 ***	$F_{4,532}$ = 48.9 ***	$F_{4,532}$ = 40.4 ***
		November	$F_{4,717}$ = 57.9 ***	$F_{4,717}$ = 58.1 ***	$F_{4,717}$ = 62.3 ***	$F_{4,717}$ = 63.7 ***
		December	$F_{4,737}$ = 218 ***	$F_{4,737}$ = 218 ***	$F_{4,737}$ = 193 ***	$F_{4,737}$ = 145 ***
		January	$F_{4,702}$ = 276 ***	$F_{4,702}$ = 224 ***	$F_{4,702}$ = 164 ***	$F_{4,702}$ = 116 ***
		February	$F_{4,667}$ = 316 ***	$F_{4,667}$ = 300 ***	$F_{4,667}$ = 240 ***	$F_{4,667}$ = 166 ***
		April	$F_{4,257}$ = 14.1 ***	$F_{4,257}$ = 18.5 ***	$F_{4,257}$ = 25.4 ***	$F_{4,257}$ = 23.7 ***
Intraspecific consistency	Species		$F_{2,87}$ = 26.1 ***	$F_{2,87}$ = 35.3 ***	$F_{2,87}$ = 16.3 ***	$F_{2,87}$ = 8.5 ***
Inter-island consistency	Species x Island		$F_{1,103}$ = 0.1	$F_{1,103}$ = 0.06	$F_{1,103}$ = 0.005	$F_{1,103}$ = 0.8
	Species		F1,103 = 11.6 ***	F1,103 = 8.7 **	F1,103 = 4.0 *	F1,103 = 2.3
	Island		F1,103 = 0.1	F1,103 = 0.02	F1,103 = 0.005	F1,103 = 1.1

Appendix 5-2. Summary of distances (km) between centroid of monthly auklet percent volume contours and the main northern ice pack; mean +/- SD (sample size).

		Crested Auklets			
		90% Volume Contour	75% Volume Contour	50% Volume Contour	25% Volume Contour
Aug	Buldir	903 +/- 279 (16)	811 +/- 290 (16)	733 +/- 290 (16)	714 +/- 401 (16)
	Gareloi	836 +/- 290 (8)	699 +/- 256 (8)	624 +/- 282 (8)	569 +/- 325 (8)
Oct	Buldir	538 +/- 425 (37)	511 +/- 429 (37)	464 +/- 433 (37)	444 +/- 427 (37)
	Gareloi	467 +/- 488 (11)	408 +/- 410 (11)	367 +/- 430 (11)	472 +/- 587 (11)
Nov	Buldir	1630 +/- 490 (55)	1734 +/- 517 (55)	1896 +/- 561 (55)	1981 +/- 623 (55)
	Gareloi	1534 +/- 509 (35)	1608 +/- 553 (35)	1727 +/- 647 (35)	1780 +/- 718 (35)
Dec	Buldir	2271 +/- 412 (54)	2277 +/- 410 (54)	2283 +/- 409 (54)	2288 +/- 411 (54)
	Gareloi	2156 +/- 511 (40)	2161 +/- 509 (40)	2158 +/- 505 (40)	2156 +/- 509 (40)
Jan	Buldir	1730 +/- 422 (51)	1742 +/- 431 (51)	1756 +/- 453 (51)	1766 +/- 469 (51)
	Gareloi	1733 +/- 479 (37)	1743 +/- 479 (37)	1753 +/- 482 (37)	1767 +/- 496 (37)
Feb	Buldir	1757 +/- 629 (49)	1759 +/- 634 (49)	1755 +/- 632 (49)	1743 +/- 661 (49)
	Gareloi	1778 +/- 727 (30)	1781 +/- 723 (30)	1792 +/- 717 (30)	1797 +/- 711 (30)
Apr	Buldir	1029 +/- 653 (5)	1118 +/- 749 (5)	1175 +/- 740 (5)	1222 +/- 722 (5)
	Gareloi	996 +/- 254 (2)	954 +/- 156 (2)	980 +/- 140 (2)	1004 +/- 111 (2)

		Parakeet Auklets			
		90% Volume Contour	75% Volume Contour	50% Volume Contour	25% Volume Contour
Aug	Buldir	1597 +/- 440 (45)	1567 +/- 439 (45)	1530 +/- 452 (45)	1508 +/- 472 (45)
	Gareloi	1817 +/- 256 (18)	1747 +/- 269 (18)	1664 +/- 274 (18)	1629 +/- 279 (18)
Oct	Buldir	1373 +/- 370 (46)	1364 +/- 368 (46)	1360 +/- 379 (46)	1363 +/- 389 (46)
	Gareloi	1420 +/- 292 (17)	1398 +/- 293 (17)	1386 +/- 303 (17)	1397 +/- 308 (17)
Nov	Buldir	1315 +/- 353 (46)	1314 +/- 350 (46)	1308 +/- 349 (46)	1303 +/- 371 (46)
	Gareloi	1416 +/- 390 (18)	1419 +/- 388 (18)	1414 +/- 385 (18)	1389 +/- 408 (18)
Dec	Buldir	1326 +/- 360 (46)	1323 +/- 361 (46)	1313 +/- 380 (46)	1299 +/- 411 (46)
	Gareloi	1219 +/- 436 (18)	1221 +/- 442 (18)	1219 +/- 447 (18)	1209 +/- 452 (18)
Jan	Buldir	950 +/- 386 (46)	957 +/- 390 (46)	961 +/- 395 (46)	963 +/- 403 (46)
	Gareloi	1039 +/- 404 (18)	1035 +/- 402 (18)	1033 +/- 398 (18)	1050 +/- 384 (18)
Feb	Buldir	1048 +/- 409 (46)	1019 +/- 409 (46)	996 +/- 419 (46)	976 +/- 442 (46)
	Gareloi	1096 +/- 285 (18)	1069 +/- 292 (18)	1057 +/- 300 (18)	1043 +/- 331 (18)
Apr	Buldir	1223 +/- 418 (32)	1228 +/- 437 (32)	1245 +/- 478 (32)	1287 +/- 568 (32)
	Gareloi	1120 +/- 310 (17)	1122 +/- 332 (17)	1125 +/- 381 (17)	1128 +/- 445 (17)

Appendix 5-3. Summary of distances (km) between centroid of monthly auklet percent volume contours and the colony of origin; mean +/- SD (sample size).

		Crested Auklets			
		90% Volume Contour	75% Volume Contour	50% Volume Contour	25% Volume Contour
Aug	Buldir	1376 +/- 335 (16)	1491 +/- 357 (16)	1597 +/- 426 (16)	1626 +/- 495 (16)
	Gareloi	1514 +/- 270 (8)	1669 +/- 283 (8)	1756 +/- 340 (8)	1805 +/- 373 (8)
Oct	Buldir	1762 +/- 483 (37)	1800 +/- 481 (37)	1869 +/- 482 (37)	1906 +/- 492 (37)
	Gareloi	1863 +/- 442 (11)	1942 +/- 459 (11)	2040 +/- 519 (11)	2070 +/- 526 (11)
Nov	Buldir	1073 +/- 264 (55)	1140 +/- 284 (55)	1274 +/- 298 (55)	1389 +/- 291 (55)
	Gareloi	1439 +/- 228 (35)	1505 +/- 252 (35)	1633 +/- 303 (35)	1717 +/- 306 (35)
Dec	Buldir	1620 +/- 224 (54)	1626 +/- 220 (54)	1629 +/- 223 (54)	1633 +/- 234 (54)
	Gareloi	1912 +/- 287 (40)	1910 +/- 284 (40)	1904 +/- 283 (40)	1900 +/- 287 (40)
Jan	Buldir	1714 +/- 341 (51)	1721 +/- 345 (51)	1732 +/- 364 (51)	1741 +/- 380 (51)
	Gareloi	2068 +/- 425 (37)	2072 +/- 428 (37)	2074 +/- 434 (37)	2084 +/- 448 (37)
Feb	Buldir	1806 +/- 504 (49)	1810 +/- 505 (49)	1809 +/- 506 (49)	1804 +/- 527 (49)
	Gareloi	2199 +/- 558 (30)	2203 +/- 556 (30)	2210 +/- 553 (30)	2210 +/- 555 (30)
Apr	Buldir	1128 +/- 331 (5)	1290 +/- 443 (5)	1427 +/- 485 (5)	1525 +/- 412 (5)
	Gareloi	759 +/- 205 (2)	823 +/- 218 (2)	879 +/- 275 (2)	883 +/- 295 (2)

		Parakeet Auklets			
		90% Volume Contour	75% Volume Contour	50% Volume Contour	25% Volume Contour
Aug	Buldir	866 +/- 431 (45)	897 +/- 441 (45)	931 +/- 461 (45)	963 +/- 487 (45)
	Gareloi	735 +/- 233 (18)	793 +/- 225 (18)	862 +/- 201 (18)	891 +/- 192 (18)
Oct	Buldir	873 +/- 402 (46)	881 +/- 411 (46)	886 +/- 434 (46)	887 +/- 455 (46)
	Gareloi	948 +/- 281 (17)	966 +/- 287 (17)	971 +/- 305 (17)	955 +/- 323 (17)
Nov	Buldir	583 +/- 303 (46)	587 +/- 297 (46)	592 +/- 300 (46)	600 +/- 327 (46)
	Gareloi	655 +/- 251 (18)	653 +/- 248 (18)	670 +/- 236 (18)	765 +/- 265 (18)
Dec	Buldir	471 +/- 169 (46)	477 +/- 169 (46)	497 +/- 176 (46)	518 +/- 199 (46)
	Gareloi	561 +/- 204 (18)	570 +/- 194 (18)	578 +/- 191 (18)	587 +/- 196 (18)
Jan	Buldir	508 +/- 186 (46)	513 +/- 182 (46)	520 +/- 181 (46)	528 +/- 184 (46)
	Gareloi	562 +/- 208 (18)	560 +/- 210 (18)	556 +/- 208 (18)	550 +/- 198 (18)
Feb	Buldir	602 +/- 255 (46)	599 +/- 250 (46)	605 +/- 249 (46)	618 +/- 248 (46)
	Gareloi	635 +/- 330 (18)	630 +/- 328 (18)	621 +/- 303 (18)	638 +/- 278 (18)
Apr	Buldir	757 +/- 283 (32)	777 +/- 306 (32)	807 +/- 356 (32)	850 +/- 457 (32)
	Gareloi	621 +/- 259 (17)	636 +/- 287 (17)	673 +/- 342 (17)	729 +/- 410 (17)

		Whiskered Auklet			
		90% Volume Contour	75% Volume Contour	50% Volume Contour	25% Volume Contour
Aug	Buldir	175 +/- 103 (17)	165 +/- 100 (17)	156 +/- 101 (17)	158 +/- 101 (17)
	Gareloi	NA	NA	NA	NA
Oct	Buldir	340 +/- 197 (16)	326 +/- 185 (16)	316 +/- 163 (16)	293 +/- 139 (16)
	Gareloi	NA	NA	NA	NA
Nov	Buldir	159 +/- 147 (17)	156 +/- 147 (17)	152 +/- 151 (17)	147 +/- 148 (17)
	Gareloi	NA	NA	NA	NA
Dec	Buldir	98 +/- 75 (17)	90 +/- 78 (17)	99 +/- 71 (17)	99 +/- 81 (17)
	Gareloi	NA	NA	NA	NA
Jan	Buldir	117 +/- 73 (17)	118 +/- 72 (17)	122 +/- 64 (17)	125 +/- 68 (17)
	Gareloi	NA	NA	NA	NA
Feb	Buldir	253 +/- 167 (17)	249 +/- 170 (17)	238 +/- 183 (17)	224 +/- 205 (17)
	Gareloi	NA	NA	NA	NA

Appendix 5-4. Summary of monthly auklet use of each bathymetry zone: percent of each volume contour that overlapped with each zone; mean +/- SD (sample size).

		Crested Auklets			
	Bathymetry Zone	90% Volume Contour	75% Volume Contour	50% Volume Contour	25% Volume Contour
Aug	<50m	28 +/- 14	36 +/- 17	44 +/- 19	52 +/- 27
n=24	50-100m	24 +/- 7.7	27 +/- 9.1	28 +/- 13	26 +/- 21
	100-150m	5.0 +/- 2.8	4.0 +/- 2.9	2.4 +/- 3.2	1.5 +/- 5.1
	150-2000m	6.4 +/- 5.2	4.9 +/- 4.8	2.8 +/- 4.3	2.0 +/- 4.6
	>2000m	16 +/- 15	9.4 +/- 13	5.7 +/- 12	3.9 +/- 12
Oct	<50m	30 +/- 17	30 +/- 20	31 +/- 23	30 +/- 26
n=48	50-100m	24 +/- 11	23 +/- 12	23 +/- 15	22 +/- 21
	100-150m	7.7 +/- 12	8.7 +/- 12	9.4 +/- 16	8.7 +/- 17
	150-2000m	13 +/- 15	15 +/- 18	18 +/- 26	21 +/- 33
	>2000m	7.5 +/- 14	6.0 +/- 13	3.8 +/- 11	2.7 +/- 12
Nov	<50m	8.7 +/- 8.7	8.4 +/- 9.8	8.0 +/- 11	8.1 +/- 13
n=90	50-100m	8.7 +/- 6.5	8.9 +/- 6.5	8.3 +/- 7.6	9.3 +/- 12
	100-150m	3.5 +/- 2.7	3.9 +/- 3.1	4.1 +/- 3.9	4.1 +/- 5.1
	150-2000m	20 +/- 10	22 +/- 12	28 +/- 17	35 +/- 23
	>2000m	42 +/- 22	41 +/- 24	40 +/- 27	36 +/- 30
Dec	<50m	3.0 +/- 4.5	3.0 +/- 5.0	3.0 +/- 6.8	3.2 +/- 8.4
n=94	50-100m	4.2 +/- 6.7	4.3 +/- 7.1	4.5 +/- 8.4	4.6 +/- 9.5
	100-150m	2.9 +/- 3.8	3.0 +/- 4.2	3.0 +/- 4.6	3.4 +/- 6.2
	150-2000m	46 +/- 21	48 +/- 22	50 +/- 26	51 +/- 30
	>2000m	38 +/- 26	37 +/- 27	36 +/- 28	34 +/- 31
Jan	<50m	3.3 +/- 5.1	3.3 +/- 5.6	3.5 +/- 7.5	4.1 +/- 9.8
n=88	50-100m	4.0 +/- 6.7	4.1 +/- 7.8	4.3 +/- 9.3	4.7 +/- 12
	100-150m	2.9 +/- 3.2	2.8 +/- 3.5	2.6 +/- 3.7	2.4 +/- 4.4
	150-2000m	49 +/- 23	49 +/- 26	49 +/- 29	48 +/- 34
	>2000m	34 +/- 23	35 +/- 26	36 +/- 30	37 +/- 35
Feb	<50m	3.3 +/- 3.9	3.3 +/- 4.3	3.0 +/- 4.5	2.4 +/- 4.2
n=79	50-100m	4.5 +/- 4.7	4.4 +/- 5.1	3.9 +/- 5.2	3.3 +/- 6.0
	100-150m	3.9 +/- 3.8	3.8 +/- 4.0	3.4 +/- 4.3	3.4 +/- 6.3
	150-2000m	48 +/- 25	51 +/- 27	53 +/- 30	53 +/- 35
	>2000m	29 +/- 24	28 +/- 25	28 +/- 29	29 +/- 34
Apr	<50m	1.7 +/- 2.2	1.9 +/- 2.3	2.6 +/- 3.5	3.6 +/- 5.1
n=7	50-100m	5.9 +/- 8.8	6.3 +/- 9.6	7.0 +/- 11	8.2 +/- 12
	100-150m	3.3 +/- 4.4	3.9 +/- 5.5	5.6 +/- 7.9	6.2 +/- 11
	150-2000m	11 +/- 9.0	12 +/- 11	14 +/- 15	16 +/- 18
	>2000m	76 +/- 26	73 +/- 29	65 +/- 38	60 +/- 45

		Parakeet Auklets			
	Bathymetry Zone	90% Volume Contour	75% Volume Contour	50% Volume Contour	25% Volume Contour
Aug	<50m	11 +/- 16	12 +/- 18	13 +/- 21	13 +/- 23
n=63	50-100m	18 +/- 15	18 +/- 17	19 +/- 20	21 +/- 25
	100-150m	11 +/- 9.5	13 +/- 12	14 +/- 16	16 +/- 22
	150-2000m	12 +/- 7.4	12 +/- 9.0	13 +/- 12	15 +/- 16
	>2000m	43 +/- 30	40 +/- 31	36 +/- 34	32 +/- 36
Oct	<50m	9.1 +/- 15	9.5 +/- 17	9.8 +/- 19	9.3 +/- 21
n=63	50-100m	11 +/- 16	11 +/- 17	11 +/- 20	12 +/- 25
	100-150m	4.1 +/- 8.1	3.8 +/- 9.0	3.4 +/- 9.1	2.6 +/- 8.0
	150-2000m	11 +/- 8.4	11 +/- 11	11 +/- 15	11 +/- 19
	>2000m	54 +/- 35	55 +/- 37	57 +/- 40	59 +/- 43
Nov	<50m	3.2 +/- 8.0	3.0 +/- 82	2.9 +/- 8.6	2.5 +/- 8.7
n=64	50-100m	6.5 +/- 14	6.9 +/- 15	6.5 +/- 16	6.4 +/- 20
	100-150m	2.9 +/- 8.0	2.9 +/- 8.7	3.0 +/- 10	3.0 +/- 11
	150-2000m	8.1 +/- 6.4	7.0 +/- 7.7	6.6 +/- 9.9	6.1 +/- 13
	>2000m	76 +/- 29	77 +/- 30	78 +/- 32	79 +/- 35
Dec	<50m	0.6 +/- 1.8	0.5 +/- 1.8	0.5 +/- 2.0	0.5 +/- 2.2
n=64	50-100m	2.9 +/- 11	3.0 +/- 12	3.5 +/- 14	4.3 +/- 17
	100-150m	1.4 +/- 4.2	1.2 +/- 4.2	1.2 +/- 5.7	1.2 +/- 8.0
	150-2000m	6.9 +/- 5.3	5.9 +/- 5.8	5.4 +/- 8.5	5.5 +/- 12
	>2000m	88 +/- 17	89 +/- 18	89 +/- 21	88 +/- 25
Jan	<50m	0.4 +/- 0.8	0.4 +/- 0.7	0.4 +/- 0.8	0.3 +/- 0.8
n=64	50-100m	1.3 +/- 4.5	1.2 +/- 4.1	1.2 +/- 3.1	0.9 +/- 2.5
	100-150m	1.2 +/- 4.1	1.1 +/- 4.4	1.3 +/- 5.7	1.6 +/- 7.1
	150-2000m	6.0 +/- 6.9	5.9 +/- 8.2	6.4 +/- 11	7.4 +/- 15
	>2000m	91 +/- 15	91 +/- 16	91 +/- 18	90 +/- 21
Feb	<50m	0.6 +/- 1.4	0.6 +/- 1.8	0.6 +/- 2.1	0.5 +/- 1.4
n=64	50-100m	0.9 +/- 1.2	0.9 +/- 1.1	0.9 +/- 1.6	0.9 +/- 2.0
	100-150m	0.8 +/- 0.9	0.8 +/- 0.9	0.7 +/- 1.2	0.7 +/- 1.6
	150-2000m	5.9 +/- 6.1	5.8 +/- 7.0	5.4 +/- 8.1	5.3 +/- 9.8
	>2000m	91 +/- 11	91 +/- 12	91 +/- 14	91 +/- 18
Apr	<50m	0.4 +/- 0.8	0.3 +/- 0.9	0.4 +/- 1.5	0.5 +/- 2.6
n=49	50-100m	1.0 +/- 2.0	0.9 +/- 2.3	0.9 +/- 3.3	1.0 +/- 5.2
	100-150m	0.7 +/- 1.1	0.6 +/- 1.3	0.6 +/- 1.8	0.6 +/- 2.5
	150-2000m	5.5 +/- 5.5	4.5 +/- 5.6	3.3 +/- 5.9	2.7 +/- 6.3
	>2000m	92 +/- 9.7	93 +/- 10	94 +/- 13	95 +/- 16